

***Lichenomphalia umbellifera*: fungible and infungible epithets and species concepts**

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ABSTRACT—Comparison of the protologue of *Agaricus umbellifer* L. with specimens and descriptions of the basidiolichen *Lichenomphalia umbellifera* (L.) Redhead & al. revealed that the epithet *umbellifera* was misapplied to the *Lichenomphalia* species, causing several major conflicts with Linnaeus's species concept. A felicitous match for Linnaeus's species concept was found with a species of *Marasmius* sect. *Epiphylli*. Because *A. umbellifer* falls in a group that arises from an evolutionary pathway divergent from that leading to *Marasmius* s. str., we erected a new genus, *Owingsia*, to accommodate it, and recombined the type species as *Owingsia umbellifera*. Molecular studies demonstrated that it is a widely distributed circumpolar species, prevalent in Lapland and islands of the Baltic Sea, where Linnaeus encountered it. The earliest legitimate description of the basidiolichen *L. umbellifera* is *A. pseudoandrosaceus* Bull., a name superseded by the sanctioned later synonym, *A. ericetorum* Pers. We recombined this basionym as *L. ericetorum*, and epitypified *O. umbellifera* and *L. ericetorum* with modern sequenced specimens.

KEY WORDS—nomenclature, taxonomy

Introduction

How serious the conflict must be before a lectotypification can be superseded is a matter of opinion . . . —JØRGENSEN & RYMAN, 1994

The nomenclatural type is not necessarily the most typical or representative element of the taxon. —THE SHENZHEN CODE, ART. 7.2

The basidiolichen currently known as *Lichenomphalia umbellifera* is distributed throughout the Northern Hemisphere (Geml & al. 2012). Because it prefers northern barrens over other habitats, it is ubiquitous in the Canadian province of Newfoundland and Labrador (NL), and the authors know it well: authors AV & GT have collected it in NL for some 20 years and author IS knows it from her native Estonia. AV can find it regularly about one hour's walk from his front door, on Mt. Ignoble, a hilltop laid barren by forest fire almost 100 years ago. Between 2003 and 2019, Foray Newfoundland & Labrador (FNL, the provincial mushroom club) recorded it 74 times on its annual forays, and AV made 32 collections of it at other times. The basidiolichen has a very variable macroscopic appearance (FIG. 1) regarding colour, shape, and gill arrangement and attachment; basidia with 1, 2, 3, and 4 sterigmata, producing spores smaller in size as the count goes up; diverse habitat tolerance, found from arctoalpine to lowland regions, in barrens, woodlands and even a grassy road embankment; and wide substrate preferences, most prevalent in peat or *Sphagnum* L., but also fruiting on bare ground with moss, on heath, bog, and characteristically on moss-covered fallen logs.

In the early years of surveying the funga of NL, we knew the current *L. umbellifera* as *Omphalina ericetorum*. By 2006 the newly combined *L. umbellifera* (Redhead & al. 2002) had become the only name used for it on FNL species lists. We applied first one, then the other name, without question. A need to review their protologues and nomenclatural history only arose after almost two decades, precipitated by a taxonomic review of some of its synonyms (Voitek 2022): a preliminary reading of the protologue suggested that the current application of the epithet might be at odds with the original material. This study was undertaken to investigate that question formally. To clearly differentiate between Linnaeus's *Agaricus umbellifer* and the basidiolichen currently known as *Lichenomphalia umbellifera*, in our discussions we represent the basidiolichen by the contraction AM-MIN, from "Amanita minima", the first two words Linnaeus (1732) used to describe it on his first encounter.

SpeciesFungorum(<https://www.speciesfungorum.org/GSD/GSDspecies.asp?RecordID=375200>; last accessioned 13 Mar 2022) provides a quick overview of the nomenclatural history of AM-MIN: a plethora of names have been applied to the species, the earliest being *Agaricus "umbelliferus"*, introduced by Carl Linnaeus (1753). [In both Classical and Botanical Latin, the correct masculine adjective is *umbellifer*; and the orthographic variant "*umbelliferus*"



FIG. 1. Collage of several presentations of the mercurial AM-MIN in NL, also showing the fit with many descriptive names used over the years. Colour: from near-white (H, L, M), fitting with “niveus”, to yellow (D, F, G), to tan-brown (I, K), to darker or duskier (fuscous) brown (B, C, E, J). At times purplish hues visible, characteristically on the upper stipe (B, C), fitting with “luteolilacina”. Pileus near-plane (F, H, K), dome-shaped (E, F), upturned (G, I, L), or turbinate-obconical (C, D, M), minutely asperous (D, F, G). Central depression almost absent or shallow (F, H, K), narrow (C, M), or wide and deep, tapering to a sharp point (G, I, L). Lamellae adnate (H, K), to decurrent (C, D, G, L). Stipe most commonly sturdy (relatively wide), but on occasion delicate or narrow (A, K, L). Generally less than two cap diameters long, but occasionally reaches two cap diameters (I, L). Bends upwards on sides of peat pits (A, J), fitting with “turficola”. Occasionally rises with a knock-kneed curve (L), fitting with “valgus”. Usually bounteous botryoid lichen thallus readily visible at the base of the stipe (F, J), often covering neighbouring moss or sphagnum (C, D, L).

is correctable under ICN Art. 60.1 (Turland & al. 2018; henceforth the Code).] In total, AM-MIN has been referred to 19 genera, using 17 different specific epithets, and 21 different subspecific epithets, eight of which have not been used at the species level. These synonyms refer to a wide array of shapes (agaricoid, omphalinoid, umbelliferous, conical), colours (white, yellow, gray, pink, lilac), substrates (algae, turf, leaves, grass, wood), and other characters, with very little to support a uniform species concept. No doubt the mercurial nature of AM-MIN (FIG. 1) is partly responsible for some of these synonyms, but their profusion and in some cases seeming incompatibility suggests that other factors may be operational as well.

Our plan was to begin by establishing Linnaeus's concept of *Agaricus umbellifer*. Should a clear picture result, it can be tested for fit with AM-MIN. Should it fit, the name is well applied, and our quest is over. Should it not fit, we decided two tasks needed to be completed: 1) identify a fitting species to which *A. umbellifer* can be applied, and 2) find an acceptable name for AM-MIN.

Determining Linnaeus's species concept of *Agaricus umbellifer*

Method

All descriptions by Linnaeus were examined for uniform and consistent characters, to get an idea of his species concept for this name. The protologue (Linnaeus 1753) was assigned greatest authority. Blindly imposing conspecificity or synonymy on all cited descriptions by others produced illogical conflicts. For example, this approach led Redhead & Kuyper (1987) to conclude that Linnaeus (1753) included more than one species by citing a description and illustration by Micheli (1729) of a long-stemmed species with a bowl-shaped cap, while describing a flat-capped one. To claim that he cited a round-capped species as conspecific did not make sense, provided he considered cap shape an interspecific character. However, because Linnaeus did not state that he considered any of his citations conspecific or synonymous, we decided to avoid assigning an arbitrary significance to them that he may not have intended. Rather, we assumed that he selected the most accurate match he could find from a limited field of similar species in order to demonstrate major characters he considered important to *A. umbellifer*, but did not designate them as synonyms because he did not believe they were. With this approach, the citations made sense, and enabled us to use cited descriptions with some conflicting elements to note those shared characters specifically stressed by Linnaeus and other cited authors.

Linnaeus's travels to Lapland were in northern Fennoscandia (not in the modern Finnish political region of Lapland). Throughout this discussion we

interpret Lapland as the ethnocultural region Sápmi, traditionally occupied by the Sámi people, encompassing the northern parts of Norway, Sweden and Finland as well as the adjoining Kola Peninsula of Russia. Because the region has no politically defined borders, its exact extent varies with different descriptions; we used the area defined by Pinto-Guillaume (2017).

Results

TABLE 1 summarizes Linnaeus's efforts to circumscribe *Agaricus umbellifer* morphologically and ecologically. Characters of illustrated treatments are taken from both descriptions and illustrations. A character is marked present (+) only if listed or directly quoted in the work.

Linnaeus described two personal encounters with the species, the first in Lapland (Linnaeus 1737) with the phrase name *Agaricus caulescens albus parvus, petiole longo, pileo plano pellucido, margine multifidio*, and the second in Öland (Linnaeus 1741) with the phrase name *Agaricus minimus capitulo turbinato plano albo, lamellis margine fuscis*. We know he considered them conspecific because in the first edition of *Flora Suecica* (Linnaeus 1745) he quoted both these phrase names in full when describing the same entity as species #1033, with the phrase name *Agaricus caulescens, pileo plicato membranaceo lamellis basi latioribus*. As the only additional character, he added that it is found among decaying fallen leaves (*inter semiputrida dejecta folia sylvarum*). In addition to his own previous phrase names, Linnaeus (1745) quoted phrase names by Micheli (1729) and Ray (1724) in full, cited another by Haller (1742), as well as illustrations by Micheli and by Buxbaum (1733). In *Species Plantarum* (Linnaeus 1753), the work where he introduced use of binomial names, for species # 22, *A. umbellifer*, he quoted in full his phrase names from the Lapland, Öland, and the Swedish flora (Linnaeus 1737, 1741, 1745), as well as the phrase name by Micheli, again citing the latter's illustration. Under the modern Code, the starting date for valid fungal nomenclature has been set back to 1753, making the *Species Plantarum* description the nomenclatural protologue for *A. umbellifer*. As before, the only descriptive information he added was to repeat that the species occurred among piles of decaying leaves. Linnaeus's final treatment of the species came two years later in the second edition of Swedish flora (Linnaeus 1755) as species #1192. Apart from the change from the phrase name used in the first edition to the binomial, the description repeated that of the first edition.

TABLE 1. Linnaeus’s species concept of *Agaricus umbellifer*, in comparison with the neotype of *Owingsia umbellifera*

	BASIDIOMA		PILEUS			STIPE	LAMELLAE		SUBSTRATE
	WHITE	TINY	FLAT	PLICATE	STRIATE	LONG	DISTANT	BROAD	LEAFY
Linnaeus 1737	+	+	+	+	+	+	–	–	–
Linnaeus 1741	+	+	+	+	–	–	–	–	–
Linnaeus 1745	+	+	+	+	+	+	+	+	+
Linnaeus 1753 protologue	+	+	+	+	+	+	+	+	+
Linnaeus 1755	+	+	+	+	+	+	+	+	+
Ray 1724	+	+	–	–	–	+	–	–	–
Micheli 1729	+	+	–	–	+	+	+	–	+
Buxbaum 1733	+	+	–	+	–	+	–	–	–
Haller 1742	+	+	+	–	–	+	–	–	+
Total	9	9	6	6	5	8	4	3	5
<i>Owingsia umbellifera</i> neotype	+	+	+	+	+	+	+	+	+

The sum of Linnaeus’s descriptions and citations gel into a lucid concept (TABLE 1): *A. umbellifer* is a small, white mushroom with a flat, somewhat translucent, radially segmented cap, distant adnate gills, a long stem, growing on fallen leaves. A few characters deserve comment. Pellucid, membranaceous, and striate are interpreted as different ways to indicate a translucent cap with visible radial lamellar projections. We lumped these, along with plicate or a segmented margin, as descriptions of an umbrella-like pileus. The common current concept of *turbinatus* (turbinate) is a laterally obconical pileus. However, at that time *turbinatus* was also used to describe a spinning propeller-like disc of radiating wedges, like the vanes of a fan or windmill. When Linnaeus encountered AM-MIN (vide infra) he used the term *infundibuliform* to indicate its common laterally obconical cap. We believe it is significant that he did not use this term in any of his five descriptions of *A. umbellifer*, and therefore consider *turbinatus* as yet another way to describe a segmented umbrella-like cap. Size is not measured, but generally he uses *minimus*, and certainly *parvus* for species with a cap diameter around one cm or less. The stem is consistently described as long. Length is a relative term, in the case of agarics compared to cap diameter. Generally, a stem less than one cap diameter is considered short. A “normal” stem length varies from one to two cap diameters. Usually, the stem must approach or exceed three cap diameters, before “long” is used as

a reliable and unmistakable identifying character. Thus, his concept is an agaric with a stem noticeably longer than at least two and one-half cap diameters. In his formal treatments Linnaeus described the gills as broad-based, but did not describe them as decurrent. Neither cited illustration shows gill attachment; we interpret broad-based to have its usual meaning of attached adnate gills. Finally, the observation that the species grows among leaves seems significant to Linnaeus because he adds it separately on each of three occasions; such insistence should not be dismissed to indicate casual growth between random individual fallen leaves.

All cited authors lend strong support to the concept of a small white mushroom with a long stem. Two illustrations (Micheli 1729, reproduced here as FIG. 2A; Buxbaum 1733, reproduced here as FIG. 2B) indicate a mushroom with a stem considerably more than three cap diameters long. Neither has the flat cap (pileo plano, Linnaeus 1737; capitolo turbinato plano, Linnaeus 1741) described by Linnaeus on his two encounters with the species. Redhead & Kuyper (1987) commented on Micheli's description (pileo hemisphaerico), suggesting, "it appears certain that Linnaeus included more than one species in his concept", and "it may be presumed that Linnaeus included more than one

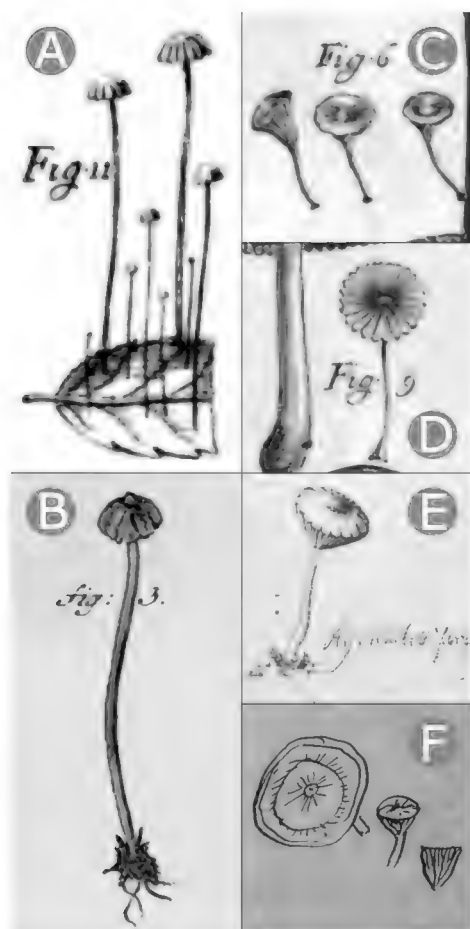


FIG. 2. Past images related or unrelated to *Agaricus umbellifer*: A. Illustration by Micheli (1729) cited by Linnaeus (1745, 1753, 1755); no doubt about the long stem and epiphyllic nature of the species; B. Illustration by Buxbaum (1733), cited by Linnaeus (1745, 1753, 1755), illustrating Linnaeus's concept of a long stem; C, D. Illustrations by Micheli (1729) available to but not cited by Linnaeus, of species much closer to AM-MIN than the image he selected; selecting the image shown in A, not the ones in C & D, shows that Linnaeus did not have an AM-MIN-like species in mind for his epithet *umbellifer*; E. Rudbeck's unlabelled illustration from his tour of Lapland (Anfält 1987), believed to represent AM-MIN; F. Linnaeus's sketch in his log of his tour of Lapland (Fries 1913), which he described with a phrase name, also believed to represent AM-MIN; note the similarity of E & F (and their similarity to C & D, but significant difference from A & B); clearly both Linnaeus and his mentor Rudbeck were familiar with AM-MIN; neither E nor F was cited in the description of *A. umbellifer*, again demonstrating that AM-MIN was not Linnaeus's species concept of *A. umbellifer*.

species in his concept as suggested by the synonymized descriptions.” Because Linnaeus repeatedly described the cap as flat, it is unlikely that he selected these illustrations as good examples of conspecificity. Rather, we suspect (but cannot prove) that Linnaeus chose these to stress the concept of a long stem. Likely a second reason for choosing Micheli’s illustration was because it clearly illustrates the epiphyllic nature of the species, the same reason Linnaeus cited Haller (1742), who described a small white mushroom arising **from** (out of) decomposing beech leaves (**ex** folio fagino putrido). Linnaeus’s “inter folia” has been interpreted to mean among (in the sense of between) leaves rather than on them (Jørgensen & Ryman 1994), a point of view that does not fit comfortably with four observations. First, Jørgensen & Ryman themselves state that Linnaeus’s attention to ecological detail was lax. Hence, the difference between “among”, “on”, and “from” may be part of this laxity, in which case assigning literal interpretation may lead to error. Secondly, it is clear that, lax or not, the association with leaves was significant to Linnaeus, because he repeated this character in all three formal treatments (Linnaeus 1745, 1753, 1755) giving it extra stress by inserting it separately at the end of each description, the only character that he felt important enough to add separately to the phrase names. Thirdly, in the protologue Linnaeus (1753) specified growth on **piled** decomposing leaves (folia **congesta**, semiputrida), a situation where growing on, rather than between leaves seems unavoidable. Finally, part of the reason Linnaeus selected certain works to cite must be because their descriptions or illustrations show features of the species he was trying to describe. That he cited Haller’s description of an epiphyllic species twice and Micheli’s similar illustration three times cannot be dismissed as random.

Linnaeus’s experience adds two further characters to the species concept: somewhat uncommonly seen, yet sufficiently distinctive to be memorable. Linnaeus described only two encounters with the species he named *A. umbellifer* in nine years, once in Lapland and once in Öland; hence not overly common. Despite the nine-year hiatus between these encounters, he seemed to have recognized the species readily the second time; hence quite distinctive.

Testing the fit of Linnaeus’s concept with AM-MIN

TABLE 2 compares Linnaeus’s species concept of *A. umbellifer*, as developed above, with AM-MIN. They differ in shape, size, and colour, and have conflicting differences in stem length (relative to cap diameter) and substrate preference. While some of the differences in characters have been

the subject of past debate, this analysis leaves little doubt about their validity. The number of irreconcilable major characters between *A. umbellifer* and AM-MIN makes it clear that Linnaeus had a species other than AM-MIN in mind for *A. umbellifer*.

Table 2. Comparison of Linnaeus’s species concept of *Agaricus umbellifer* and AM-MIN

	Basic color	Cap diameter	Cap shape, commonest	Stem length	Gill spacing	Substrate, preferred
<i>Owingsia umbellifera</i>	White	≤1 cm	Flat	≥3× cap diam.	distant/reduced	dead leaves
AM-MIN	Yellowish	>1 cm	Funnel	≤1.5× cap diam.	moderate	turf

The above is not a new discovery or an original conclusion. Redhead & Weresub (1978) documented it, and Redhead & Kuyper (1987), looking at the same information discussed here, came to the same conclusion. Further, they demonstrated that had Linnaeus wished to apply *A. umbellifer* to AM-MIN, he had images of species with an omphalinoid pileus and shorter stipe (two reproduced here as FIGS 2C & 2D) available to him among Micheli’s illustrations (Micheli 1729), that were far more AM-MIN-like than the one he chose (reproduced here as FIG. 2A).

Surely the most compelling evidence, not discussed earlier, that Linnaeus did not consider *A. umbellifer* to be AM-MIN, is that both Linnaeus and his mentor, Olof Rudbeck, **knew** AM-MIN. Both had undertaken Lapland journeys, where both had seen this iconic species of northern heaths, and both had made readily identifiable sketches of it in their respective logs. Rudbeck’s 1695 log, *Iter Lapponicum—skissboken från resan till Lappland*, was published posthumously (Anfält 1987). There is no evidence that Rudbeck described or named the species, but he left an illustration (reproduced here as FIG. 2E). Linnaeus’s log of 1732, also entitled *Iter Lapponicum*, was also published posthumously and translated into several languages; we refer to the second Swedish translation by T.M. Fries (1913). In his log Linnaeus left an illustration (reproduced here as FIG. 2F) with a descriptive phrase name, *Amanita minima, infundibuliformi plana, lamellis alternis integris, bifurcates, alternis semi, alba*, the source (as mentioned) for our contraction AM-MIN. Note that Linnaeus applied *Amanita* quite differently from its current usage. The name was introduced by Dillenius (1719) for one of four genera of fungi, the genus with pileus, stipe, and lamellae—in other words the group we now refer to as agarics. Linnaeus admired Dillenius, spent a month with him in

Oxford, and often followed his classification. As we have seen, Linnaeus had no difficulty citing his own observations, or those of others, so that omitting both his mentor's and his own observations of AM-MIN should end any speculation that he intended to apply *A. umbellifer* to AM-MIN. All Linnaeus's descriptions and citations were intentional, carefully chosen to circumscribe the characters of his species concept accurately and precisely; the evidence that they should not be dismissed as random events due to oversight seems overwhelming. The conflict of AM-MIN with the original description of *A. umbellifer* leads us to conclude that both earlier lectotypifications of this name (*vide infra*) should be rejected according to Art. 9.19(c) of the Code.

Why then, after rather clear demonstration by Redhead & Weresub (1978) and Redhead & Kuyper (1987) that applying Linnaeus's epithet to AM-MIN was incompatible with the protologue, did this epithet still get applied to AM-MIN? Two years after Redhead & Kuyper's opinion, where they typified *A. umbellifer* with the illustration by Micheli cited by Linnaeus, Jørgensen & Ryman (1989) proposed Rudbeck's aquarelle of AM-MIN (reproduced here as FIG. 2E), as lectotype for *A. umbellifer*, stating, "Judging from the **descriptions** and the **circumstances** (cf. Linnaeus 1737: 352, point 1) it is likely that Linnaeus based the description entirely on this drawing." Coming to this debate over 30 years later, without prejudice for either side (until we began this enquiry, we had accepted *Lichenomphalia umbellifera* as the appropriate name for AM-MIN, and had not been aware of this controversy), we developed Linnaeus's species concept from his writings (TAB. 1), and compared that with AM-MIN (TAB. 2), which led us to conclude that Linnaeus's description of *A. umbellifer* does not fit AM-MIN. Consequently, we cannot agree with Jørgensen & Ryman (1989) that Linnaeus's **descriptions** suggest this drawing was used to create the protologue. The **circumstances** Jørgensen & Ryman (1989) refer to, citing Linnaeus's introduction to the section dealing with *Fungi* in his *Flora Lapponica*, consist of references by Linnaeus to a fire that destroyed many books and good source material, and grateful expressions of relief that many of Rudbeck's illustrations had been kept safe from fire. Linnaeus thanks Rudbeck for putting these ("eos", note the plural) at his disposal. Thus, certainly Linnaeus acknowledges the availability of Rudbeck's material for his book, but speaks of illustrations in the plural (as do Jørgensen & Ryman), and nowhere does Linnaeus mention that any particular illustration was used for the description of any particular species. There is no record from Linnaeus or others that Rudbeck's unnamed and unpublished drawing of an undescribed

species—or any particular illustration—was the basis for species #471 in his *Flora Lapponica*, the protologue, or elsewhere. There is a vast gap between having **several** illustrations at one's disposal, and using one specific illustration to describe one specific species. Nothing in Jørgensen & Ryman's subsequent two paragraphs support their changing the probable "it is likely" in the above quote to the certain, "we have also **proved**" that Linnaeus had AM-MIN in mind when describing *A. umbellifer*—in fact, quite the opposite—and we find nothing to support referring to Rudbeck's drawing as "original material" for *A. umbellifer*.

We do not claim that Linnaeus did not have access to Rudbeck's Lapland material, including the drawing under question. The logical assumption would be entirely opposite. Olof Rudbeck fil. (1660–1740) was a Swedish scientist and explorer, who joined an expedition to Lapland commissioned by the King of Sweden. At that time Lapland still had the draw of terra incognita, even in Scandinavia. Unfortunately, most of Rudbeck's collections and many records from that journey were lost in a fire, but some paintings and his journal-sketchbook survived to be published posthumously. Rudbeck was mentor to the young Linnaeus, when the latter began his pursuit of botany and medicine. It is easy to imagine that the exciting tales of the mentor, supplemented by notes and illustrations, kindled enthusiasm for Lapland in his young student. Our guess is that Rudbeck made the material available to Linnaeus already before the latter's own Lapland journey, and possibly these helped spur the 25-year-old Linnaeus to undertake a Lapland journey of his own. It is equally reasonable to assume that his mentor continued to share his tales, notes, and records of the earlier journey with his protégé after the latter's return, earning him the thanks noted by Jørgensen & Ryman. Also, there is no reason to doubt that the unpublished material that Rudbeck put at Linnaeus's disposal contained the lovely illustration of AM-MIN. The description of species #471, however, especially of its long stem and its substrate, does not fit Rudbeck's illustration (stem measured just under 1.5× cap diameter, substrate seeming to be mossy soil), making it extremely difficult to accept that one was based on the other.

While we find no similarity between Linnaeus's description of *A. umbellifer* and Rudbeck's illustration, we note the uncanny similarity of Rudbeck's illustration (reproduced here as FIG. 2E) to Linnaeus's sketch of AM-MIN (reproduced here as FIG. 2F) in the log of his own Lapland journey. Linnaeus's notes described AM-MIN as infundibuliform, which fits both his and Rudbeck's

sketches, but neither he nor authors he cited ever used that term to describe *A. umbellifer*. Linnaeus made no suggestion then or later that this sketch represents his concept of *A. umbellifer*. The two logbooks offer clear proof that both Rudbeck and Linnaeus knew AM-MIN, but that it was not the species to which Linnaeus applied the binomial *Agaricus umbellifer*. Such suggestions were made later by others. In the case of Rudbeck's illustration, somebody other than Rudbeck wrote, "*A. umbelliferus* L. Fl. Su. v II 1192" on the illustration, referring to *Agaricus umbellifer*, species #1192, p. 440, in Linnaeus's *Flora Suecica* vol. 2 (Linnaeus 1755). Jørgensen & Ryman (1989) quoted Nilsson's opinion (Nilsson 1987) that this was added by the botanist Carl Johan Hartman, either 1811–1814 or 1841. Our guess is that this was not a novel idea by Hartman, but that he was influenced in this by a common misunderstanding that Fries (1821) synonymized *Agaricus ericetorum* Pers. with *A. umbellifer* L. (vide infra). If that is so, and if those are the only possible dates of the annotation, then the likely year was 1841. In the case of Linnaeus's sketch in his *Iter Lapponicum*, the species is identified as "*Agaricus (Omphalia) umbellifer* Fr." not by Linnaeus, but by T.M. Fries in his 1913 Swedish translation. Parenthetically, it is worth noting that there is no valid taxon, "*A. umbellifer* Fr." Fries treated the species twice (Fries 1825, 1828), and both times made it clear that he was referring to the taxon of Linnaeus.

Both Redhead and Kuyper remained silent, effectively ending the debate. It took over a decade before Redhead, with different collaborators (Redhead & al. 2002), published a major revision of omphalinoid genera, which required, inter alia, nomenclaturally suitable type species to be assigned to *Arrhenia* and *Omphalina*, while circumscribing AM-MIN as the type species for their newly erected genus, *Lichenomphalia*, created for lichenized omphalinoid basidiomycetes. This was accomplished by synonymizing and otherwise resolving various competing names and interpretations for *A. umbellifer* and *A. ericetorum*. To do this, they took advantage of a recent change to the International Code of Botanical Nomenclature (Greuter & al. 2000), which now permitted acceptance of the lectotype declared by Jørgensen & Ryman, namely Rudbeck's illustration. Redhead & al. rejected Redhead & Kuyper's earlier typification of *A. umbellifer*, and accepted Jørgensen & Ryman's instead, thereby applying the epithet coined by Linnaeus to AM-MIN. This contrivance avoided debate in solving the systematics of the genera involved—including getting smooth acceptance of their new genus *Lichenomphalia*—at the expense of ignoring

interspecific characters of morphological diversity. Neither Redhead & Kuyper, jointly or separately, nor Redhead and his new collaborators, ever mentioned, challenged, rebutted, refuted, or withdrew Redhead & Kuyper's published observations regarding the painfully catachrestic application of *umbellifer* to AM-MIN. Further, Redhead & al. (2002) did not embrace Jørgensen & Ryman's claim that the Rudbeck sketch was the only image on which Linnaeus based his description of *A. umbellifer*. Rather, they noted the sketch had been "APPARENTLY available to Linnaeus." This statement certainly did not support the claim that the illustration was part of the original material, and Redhead & al. (2002) offered no discussion whether such availability equated to being even a partial source, let alone the **sole** source for Linnaeus's conflicting description. Further, they did not claim the epithet fit the description in any way, but rather referred to it as a "**compromise**", one they hoped would "resolve and end a 250-year old controversy over these names." Thus, the problems created by accepting *A. umbellifer* as the basionym of AM-MIN remained exactly as Redhead & Kuyper (1987) had outlined them earlier (and we confirmed here): the epithet remained misapplied to AM-MIN.

In summary, *Agaricus umbellifer* was lectotypified by Jørgensen & Ryman (1989) in the belief that the designated lectotype, Rudbeck's unnamed and unpublished (in his lifetime) 1695 illustration, was part of the original material on which Linnaeus based his protologue description. After careful study, we have found no evidence to substantiate this belief. All available evidence supports the diametric view, namely that Linnaeus did not base his description on this illustration, and had a considerably different species in mind for the name. That this must be so is confirmed by the major conflicts produced from the (mis) application of *A. umbellifer* to its declared lectotype. Subsequent acceptance of that lectotypification by Redhead & al. (2002) did not alter its legitimacy, because all available evidence still suggested that Rudbeck's illustration was not the original material for the protologue of *A. umbellifer*, and Linnaeus did not use it as a basis for his protologue—a matter, as pointed out, that Redhead & al. (2002) were careful to skirt. We reject this lectotype by Jørgensen & Ryman because there is no evidence it was used as original material by Linnaeus, and it is in major conflict with Linnaeus's protologue description. This rejection automatically rejects the subsequent adoption of Rudbeck's illustration as lectotype by Redhead & al.

One earlier lectotype remains to be considered. In his *Systema Mycologicum*, Fries (1821: 160) had referred Micheli's illustration, cited by Linnaeus, to *A. capillaris* Schum. [$\equiv$ *Mycena capillaris* (Schum.) P. Kumm.]. Both drawing and description seem to fit that species. Redhead & Kuyper (1987) proposed Micheli's illustration as lectotype for *A. umbellifer*. The illustration shows a hemispheric cap and the description states "capitolo haemispherico"—the very character that caused Redhead & Kuyper to wonder whether Linnaeus embraced more than one species in his concept! We reject this lectotypification because it contradicts the protologue description, a contradiction emphasized but not resolved by the proposing authors.

Search for a species to fit Linnaeus's concept of *Agaricus umbellifer*

Background

On a trip to Lapland in 2006, the senior author collected a small white epiphyllic agaric with a membranaceous, translucent, flat, umbrella-like segmented cap, and distant gills, supported by a long white stem, arising from that year's fallen leaves of *Populus tremula* L. (FIG. 3). He identified the collection tentatively as *Marasmius tremulae* Velen. and placed it in his personal herbarium. There it remained as collection 06.10.04.av01, altogether forgotten until this study gave rise to a lucid picture of Linnaeus's species concept of *A. umbellifer*. Immediately, this collection came to mind. On review, the collection shared all the criteria of Linnaeus's *A. umbellifer* (TAB. 1, bottom row), including the shape of the cap, which had been a problem in the past. To learn whether this species, fitting Linnaeus's description, could be the species Linnaeus described, we undertook to determine whether the species is prevalent in the regions explored by Linnaeus; in other words, is it likely that Linnaeus would have encountered this same species?



FIG. 3. *Owingsia umbellifera* (A–D = neotype, O-F-76596; E–I = TUF118289): A: Basidiomata on fallen leaves of *Populus tremula*. Note the white, flat, pellucid, umbrella-like caps, long stem, equal to about three cap diameters, widely spaced gills, broader at their base, and the many white rhizomorphs/sterile stipes. B: Neotype collection exsiccatum. C: Basidia, mostly four-spored, with about 15% 2-spored (not due to focal length artefact). D: Cystidia. E: Cheilocystidia. F: Pleurocystidia. G: Caulocystidia. H: Pileocystidia. I: Pileipellis elements. Scale bars: A, B = 5 mm; C, D = 5 μ m; E–I = 25 μ m.

Method

Collections identified as *M. tremulae* or *M. epiphyllus* (Pers.) Fr. from Lapland, Öland, and surrounding areas, augmented by a few from other regions (TAB. 3), were sought for molecular studies. Related sequences deposited in GenBank and UNITE (Kõljalg & al. 2013, Nilsson & al. 2019) were added to the analysis to construct the phylogeny (FIG. 4). ITS-DNA processing followed Voitek & al. (2020) and phylogenetic analysis Voitek & al. (2022). New sequences were deposited in UNITE and/or GenBank. Specimens were vouchered in the Herbarium, University of Oslo, Norway (O), the Fungarium, University of Tartu, Estonia (TUF), and the Herbarium, University of Western Ontario, London, Canada (UWO).

TABLE 3. Collections and sequences used in phylogenetic analyses. Neotype in bold print.

SPECIES	Country	FUNGARIUM NO. (DUPLICATE NO.)	ITS	PUBLICATION
<i>Owingsia umbellifera</i>	Czech Rep.	BRNM695733	FN293008	Antonín & al. 2010
	Czech Rep.	PRM902346	FN293010	Antonín & al. 2010
	Czech Rep.	PRM894159	FN293012	Antonín & al. 2010
	Estonia	TUF106979	UDB015277	UNITE
	Estonia	TUF118289	UDB015455	UNITE
	Estonia	TUF118453	UDB018190	UNITE
	Finland	OULU-F-16597	UDB07672480	This study
	Finland	OULU-F-16603	UDB07672482	This study
	Finland	OULU-F-16606	UDB07672483	This study
	Finland	OULU-F-24076	UDB07672485	This study
	Greenland	NN048205a	JN943599	Schoch & al. 2012
	Italy	BRNM695779	FN293007	Antonín & al. 2010
	Norway	OULU-F-21543	UDB07672484	This study
	Norway	O-F-76596 TUF117828	UDB0799033	This study
	Norway	O-F-21830	UDB036647 NOBAS2883-16	UNITE
	Poland	FeF427	MZ493079	Bilanski & Kowalski, unpubl.
	Russia	NN050222a	JN943602	Schoch & al. 2012
	Slovakia	PRM870457	FN293009	Antonín & al. 2010
	Slovakia	BRNM523367	FN293011	Antonín & al. 2010
	Sweden	UPS-F-740369	UDB07672488	This study

SPECIES	Country	FUNGARIUM NO. (DUPLICATE NO.)	ITS	PUBLICATION
<i>Owingsia</i> sp. 1	UK	K(M)40466	FN293013	Antonín & al. 2010
	USA	MF80535 NS3148	OM906872	Mohatt & al., direct sub.
	Estonia	TUF118324	UDB015484	UNITE
	Estonia	TUF118729	UDB019538	UNITE
	Finland	OULU10007053	UDB07672481	This study
	Finland	OULU-F-24077	UDB07672486	This study
<i>Owingsia</i> sp. 2	Slovakia	BRNM523372	FN293016	Antonín & al. 2010
	Canada	UWO-F3413	OP290397	This study
<i>Owingsia</i> sp. 3	Czech Rep.	BRNM695419	FN293017	Antonín & al. 2010
	Japan	soil sequence	MT594707	Favero Longo & al., unpub.
Other Physalacriaceae				
<i>Armillaria mellea</i>	—	PBM2470 AFTOL-449	AY789081	Binder & al. 2006
<i>Dactylosporina steffenii</i>	Costa Rica	TENN58785	HM005073	Petersen & Hughes 2010
<i>Desarmillaria tabescens</i>	USA	00i-99	AY213590	Kim & al. 2006
<i>Flammulina velutipes</i>	—	7200	AF030877	Hughes & al., unpub.
<i>Gloiocephala epiphylla</i>	USA	DED5971	DQ097357	Binder & al. 2006
<i>Hymenopellis radicata</i>	Sweden	TENN62837	GQ913377	Petersen & Hughes 2010
<i>Laccariopsis mediterranea</i>	Italy	MCVE23445	JX271808	Vizzini & al. 2012
<i>Mucidula mucida</i>	Austria	TENN59324	GQ844235	Petersen & Hughes 2010
<i>Paraxerula americana</i>	USA	DBG21746	HM005143	Petersen & Hughes 2010
<i>Rhizomarasmius pyrrhocephalus</i>	USA	TENN51091	DQ097369	Binder & al. 2006
<i>Rhodotus palmatus</i>	Czech Rep.	PRM889504	KC179739	Tang & al. 2014
<i>Strobilurus conigenoides</i>	USA	TENN61318	GQ892821	Petersen & Hughes 2010
<i>Xerula pudens</i>	Estonia	TUF117431	UDB031394	UNITE
Outgroup				
<i>Crinipellis scabella</i>	—	CBS243.53	MH857177	Vu & al. 2019
<i>Marasmius rotula</i>	Denmark	NN005958	JN943598	Schoh & al. 2012

^a Personal herbarium of Sara Landvik

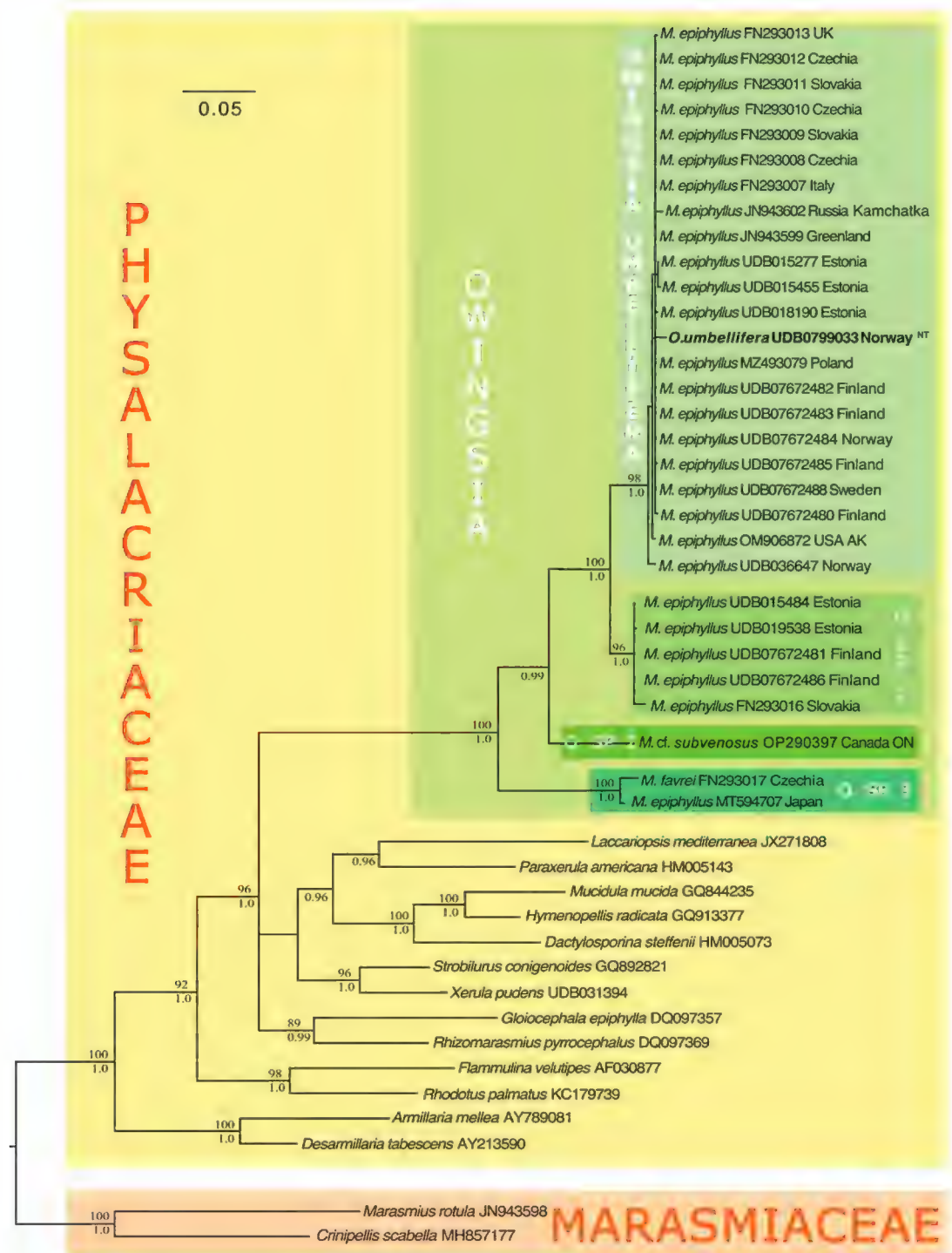


FIG. 4. ITS-based phylogenetic pathways, showing the placement of *Owingsia* in *Physalacriaceae*, here sister to *Marasmiaceae*, containing *Marasmius* s.str. Bayesian analysis shows that the genus contains *O. umbellifera* and three other clades of unidentified species to which the name *M. epiphyllus* has been applied. ML bootstrap support $\geq 70\%$ and the Bayesian posterior probabilities $\geq 95\%$ are shown above and below the branches (bs/pp), respectively. Maximal likelihood analysis revealed *Owingsia* spp. 2 and 3 in a single clade with 84% support. Sequences are identified by the name recorded on the genetic depository or fungarium accession database, with the exception of the neotype, identified by its current name. This limited sampling is inadequate to resolve the genus, a question beyond the scope of this work. *Owingsia umbellifera* is widely distributed, documented in North America from Alaska and Greenland, and in Eurasia from Scandinavia to Kamchatka. The neotype from the Norwegian part of Lapland appears in bold print. The two sister species, *O. umbellifera* and *Owingsia* spp 1, were sympatric, and several recorded on the same substrate, dead leaves of *Populus tremula*.



FIG. 5. *Owingsia* species from three of our four species clades. *Owingsia umbellifera*, Estonia: A. TUF118453; B. TUF118289; C. TUF106979. *Owingsia* sp. 1, Estonia: D. TUF118729; E. TUF118324. *Owingsia* sp. 2, Canada: F. UWO-F3413. Scale bars = 10 mm. [Photos A–E courtesy of Vello Liiv.]

Results

Bayesian analysis (Ronquist & al. 2012) showed that *Marasmiaceae*, containing the genus *Marasmius*, formed a sister clade to *Physalacriaceae*, where our specimen fell, with 29 other sequenced specimens, which split among four species (Figs 4, 5). No other collections were identified as *M. tremulae* and 27 of the 30 were identified as *M. epiphyllus*. Maximum likelihood analysis (Stamatakis 2014) of the same material placed species 2 and species 3 into a single clade with 84% support. The genus where these sequences clustered is undescribed, but sequences from other studies indicated that this clade has been identified as *Marasmius* sect. *Epiphylli* Kühner in various studies (Owings 1997, Owings &

Desjardin 1997, Wilson & Desjardin 2005, Jenkinson & al. 2014). Our collection from the Norwegian part of Lapland fell into the largest species clade with 21 other specimens, distributed widely throughout the Northern Hemisphere: from Alaska to Greenland in North America, and from Scandinavia to Kamchatka in Eurasia, with additional collections from central Europe. FIGURE 6 plots collections of this species from both regions where Linnaeus recorded it, Lapland and the Baltic Sea. Unfortunately, two relatively recent collections from Öland failed to yield amplifiable DNA, but collections from nearby Saaremaa and the west coast of Estonia produced sequences that fell into the same clade. The species is sister to a small clade of five collections, with which it shares morphology (as evidenced by the application of the same name), distribution in Lapland, and substrate preference (fallen leaves of *Populus tremula*).

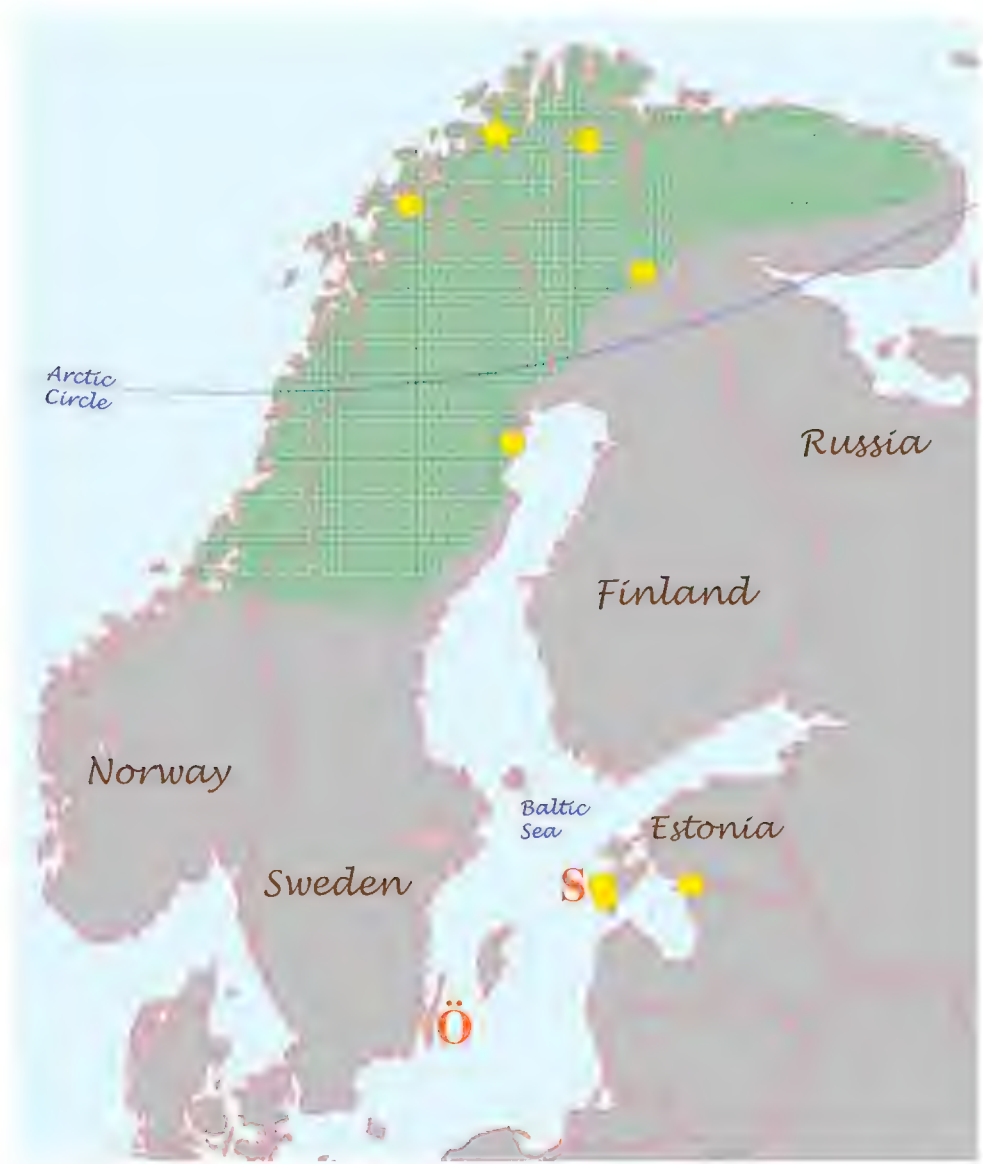


FIG. 6. Map of Fennoscandia and environs, showing the origin of sequenced specimens of *Owingsia umbellifera* (yellow circles; star for neotype) from the two sites where Linnaeus collected them, Lapland (green hatching) and Öland (Ö). Specimens from Öland did not yield DNA, but specimens from nearby Saaremaa (S), and the west coast of continental Estonia, both in the Baltic Sea, are shown instead.

Comments

Our investigations confirm and add further supporting evidence to past conclusions that the epithet *umbellifera* is misapplied to its current taxon. We were unable to substantiate previous claims to the contrary. We identified a species that matched Linnaeus's concept without conflict, and confirmed its prevalence in the same regions where Linnaeus collected his *A. umbellifer*. In our brief survey of likely candidates, this species is the most common among several similar species we now know to exist in the group, and a review of FIG. 5 suggests this species has the longest stipe of the group (i.e., most closely resembles the illustrations chosen by Linnaeus to show this character of his species). These two observations make it most likely that of the group of similar species, this was probably the one seen and described by Linnaeus with the name *A. umbellifer*. These observations do not require further comments. However, how to handle them in a work devoted to the nomenclature of two epithets warrants contemplation.

Initially we recombined *A. umbellifer* into *Marasmius*, but discussion during the review process convinced us that this was less than optimal, given the phylogenetic distance of *Marasmius* s. str. from this genus. In an unpublished Master's thesis, Owings (1997), using the LSU marker, first showed that *Marasmius*, as known at that time, was a polyphyletic genus, and, inter alia, that species of *Marasmius* sect. *Epiphylli*, along with some other genera, followed a divergent evolutionary pathway to the *Physalacriaceae*. She reported these findings with her supervisor in an abstract (Owings & Desjardin 1997), and her observations have been confirmed in various LSU-based studies of the *Physalacriaceae* (e.g., Wilson & Desjardin 2005, Ronikier & Ronikier 2011, Vizzini & al. 2012, Jenkinson & al. 2014). Multilocus analysis by Matheny & al. (2006) confirmed that *Marasmiaceae* and *Physalacriaceae* form separate provisional families arising in what they named the marasmiod clade, one of six major clades of *Agaricales*. Classifying *Marasmius*, Kühner (1933) named "*M. sect. Epiphylleae*", forming the name from *M. epiphyllus*, which he placed in the section. The Code (Art. 10.8) considers such implicit assignment of type species valid; Kühner's sectional epithet must be corrected to a masculine plural adjective, agreeing with the masculine genus (Art. 21.2) — *Marasmius* sect. *Epiphylli*.

A new genus typified by *Agaricus/Marasmius epiphyllus* would require a satisfactory typification of the species. A beginning was made by Singer (1949), who described *M. epiphyllus* as heterogenous, discussed two taxa, and then stated that he had no hesitation to designate one collection from Ulfält near

Femsjö as topotype for *M. epiphyllus*. This is a bit puzzling, because topotypes have no nomenclatural significance, and are not **designated**, but are what they are by definition: the same species from the same site where the type was collected. In this case, neither Persoon, who described *Agaricus epiphyllus*, nor Fries, who sanctioned that name and subsequently transferred it to *Marasmius*, cited a type collection, making it impossible to meet the definition. Fries did indicate that he had seen the species (v. v.), but the Code requires that a precise specimen be identified by the author for valid typification (Art. 7.11). As opposed to topotypes, neotypes must be designated. Singer did not **designate** the cited specimen as neotype, but rather stated, “we ... **recommend** it as neotype of the species.” Characteristically, Singer’s type designations are brief, clear, and unequivocal, supporting the contention that such was not his intent for *M. epiphyllus*.

Erecting a new genus with a new name and its own type species circumvents the above concerns nicely, and also avoids the need to reconcile some additional concerns. For example, Desjardin (1989) described lack of rhizomorphs as one of the characters of *M. sect. Epiphylli*, but rhizomorphs are very prominent in FIG. 3. Needless to say, the simplicity of erecting a new genus appealed to us. We shall describe briefly the new genus, *Owingsia*, recognizing that a genus created for nomenclatural convenience, without resolving its taxonomy, will not satisfy all taxonomic expectations until its taxonomy becomes settled. Taxonomic study to resolve *Marasmius* sect. *Epiphylli* is a major undertaking, requiring familiarity with the group, wide sampling and sequencing, reconciling several old names by typification, synonymization, or other means, and probably needs a global approach. For example, the different topology we noted with Bayesian and maximum likelihood analysis suggest the need for including more North American specimens, ideally with an attempt to sequence the type of *Marasmius subvenosus* Peck, and the need to include more (conservative) genetic markers in the analysis. Such work, best done by experts familiar with these species, is well beyond the scope of the stated narrow aims of this nomenclatural study. Our only reason to erect it at this time is to accommodate the new combination for *A. umbellifer* in a place more logical than *Marasmius*.

The final question warranting some comment is whether *Agaricus epiphyllus* could be a later synonym of *A. umbellifer*. Should these two sanctioned names prove to be synonymous, the normal rules of priority would apply (Art. 11.4; Art. F.3), and *A. umbellifer* would be the correct name. Pre-DNA work lacked the advantages available to us. For example, specimens FN293007–FN293013 in our phylogenetic tree are conspecific with our newly designated neotype and

were used by Antonín & Noordeloos (1993: 52–57) to describe *M. epiphyllus*. However, their specimens examined also contain FN293017 that fell into the Sp. 3 clade in our tree, and a much larger number of specimens that have not been placed phylogenetically. Earlier concepts require revision, in light of new technology, before this question can be answered. What we can say at this time, is that because our limited sequencing produced three clades to which the epithet has been applied, likely the taxonomist(s) who undertake(s) this task should have some latitude with applying the name to retain it without conflict, if desired.

Taxonomy

Owingsia I. Saar, Voitek & Thorn, **gen. nov.**

MB 845593

= *Marasmius* sect. *Epiphylli* Kühner [as “*Epiphylleae*”], Le Botaniste 25: 93. 1933.

Differs from *Marasmius* s.str. by its acollariate attached lamellae, stipe with visible vestiture, lack of broom cells, prominent cystidia, and molecular data.

TYPE SPECIES: *Owingsia umbellifera* (L.) Voitek & al.

ETYMOLOGY: Named after Pamela Owings, who first described the divergence of *Marasmius* sect. *Epiphylli* from the evolutionary pathway of the core *Marasmius* group.

Basidiomata of the four putative species clades that nestled in *Owingsia* by our ITS data (FIG. 5) are all small (cap diameter seldom over 10 mm) and whitish, with all tissues inamyloid, non-dextrinoid, and share the following characters: pileus segmented, somewhat parasol- or windmill-shaped, most commonly plane at maturity; lamellae reduced to widely spaced, acollariate, developing fold- or vein-like anastomosing ridges, developed lamellae approach the stem for a broad attachment, but within a fraction of a mm develop a sharp notch, attached to the upper stipe less broadly; stipe usually long ($>2.5\times$ cap diameter), central, pruinose, insititious; basidiospores fusiform, hyaline, without iodine reactions; cystidia present on lamellar sides and edges, on stipe, and on pileus, narrowly fusiform to narrowly lageniform, mostly with a long neck, thin-walled; pileipellis hymeniform, made up of clavate or broadly clavate, slightly to distinctly thick-walled cells; stipitipellis a cutis; epiphyllic on fallen deciduous leaves and small deciduous or herbaceous litter. Phylogenetically, our ITS data (FIG. 4) show that the genus arises from a well-supported pathway within the *Physalacriaceae* (distant from *Marasmius*, type species *M. rotula*).

SPECIMENS EXAMINED: For specimens of *O. umbellifera*, see below.

SP1: ESTONIA, SAARE, **Saaremaa**, Harilaid, 02.11.2011, Vello Liiv (TUF118324; UNITE

UDB015484); near Viidu, mixed forest, on leaves of *Populus tremula*, 08.10.2013, Vello Liiv (TUF118729; UNITE UDB019538); **FINLAND**, OUTER OSTROBOTHNIA, Ylitornio, S end of Kuusikkorommas, S part of the nature protection area, rich spruce-dominated mixed forest on calcareous ground, on leaves of *Populus tremula*, 27.09.2014, Esteri Ohenoja, Taina Romppanen, Lasse & Marja Tuominen (OULU10007053; UNITE UDB07672481); **SOMPION LAPPI**, Pelkosenniemi, Jaurujoki E, Kuotelonjoki SW, 26.08.1994, Ulla Nummela-Salo, Pertti Salo (OULU-F-24077; UNITE UDB07672486).

SP2: **CANADA**, **ONTARIO**, **Essex County**, Point Pelee National Park, West Beach, 41.9266 -82.5138, 176 m a.s.l., on fallen leaflets and rachis of *Ptelea trifoliata* in open grass-oak-juniper savannah on shoreline, 05.10.2020, P. Kelly, N.M. Weerasuriya & R.G. Thorn, RGT201005/08 (UWO-F3413; OP290397; culture DAOMC252643).

COMMENT. Formation of a distinct genetic clade within *Physalacriaceae* and congruence with *Marasmius* sect. *Epiphylli* has been confirmed by previous work (vide supra). A fuller and more exact concept of the genus awaits further taxonomic work within the group, including typification of its species.

***Owingsia umbellifera* (L.) Voitek, I. Saar & Thorn, comb. nov.**

FIG. 3

MB 845594

≡ *Agaricus umbellifer* L. [as “*umbelliferus*”], Sp. Pl. 2: 1175. 1753 (nom. sanct., Fr., Elench. Fung. 1: 22. 1828).

TYPE: **Holotype**, none. **Neotype** [here designated, MBT 10009104], Norway (Lapland), Finnmark (now Troms og Finnmark), Rafsboten, Tverrelven, 70.0159°N 23.5587°E, 47 m asl, in mixed woods on fallen leaves of *Populus tremula*, leg. Andrus Voitek 06.10.04. av01 (O-F-76596; **isoneotype** TUF117828; UNITE UDB0799033).

MACROSCOPIC. Basidioma: small, white, epiphyllic, with a thin, translucent, flat, umbrella-like pileus on a long stipe; pileus: 4–8 mm in diameter, membranaceous, translucent, plane to gently dome-shaped, becoming plane with maturity (FIGS 3A, 5B), drooping during drying (FIG. 3C, 5A, C), but on rehydration flattening out again, umbrella-like segmented, white; lamellae: distant, occasionally reduced, develop cross-veining anastomoses with age, approaching the stem for a broad attachment, but form a deep notch a fraction of a mm away from the stem (possibly by separating from it) to attach more narrowly to the upper stipe, white, acollariate; stipe: 15–26 mm high and about 1 mm wide, evenly cylindrical, straight or occasionally bent, minutely flocculose, white, with some yellow to straw colour rising from the base with maturity, insititious, associated with several white rhizomorphs or sterile stipes (FIG. 3A, B); spore print: white.

MICROSCOPIC. Basidiospores: (n = 50; 3 basidiomata, 2 collections, 2 observers) 7.7–13.5 × 3.5–6.7 μm (average 11.8 × 5.1 μm), Q = 2.0–2.9, (average 2.3),

ellipsoid-lacrymoid, hyaline, inamyloid; basidia: (n = 7) 8–11 × 42–54 µm, 4-spored, about 15% 2-spored (FIG. 3C); cystidia: plentiful and pleomorphic (FIG. 3D); cheilo- and pleurocystidia: similar (n = 18) 25–42 × 4.5–67.3 µm (average 33.5 × 5.7 µm), narrowly fusiform to lageniform, mostly with a long neck, thin-walled (FIG. 3E, F); pileocystidia: slightly larger but otherwise similar to hymenial cystidia (n = 12) 27–44 × 5.3–8.5 µm (average 38 × 6.6 µm), narrowly fusiform to narrowly lageniform, mostly with a long neck, thin-walled (FIG. 3G); caulocystidia: (n = 8) 20–26 × 4–6 µm (average 24 × 5 µm), fusiform to lageniform, thin-walled to slightly thick-walled (FIG. 3H); pileipellis: hymeniform, (n = 28) 12–26 × 6–12 µm (average 19 × 10 µm), clavate to broadly clavate, slightly to distinctly thick-walled cells (FIG. 3I); stipitipellis: a cutis of hyphae, up to 3–8 µm wide; clamp connections: in all tissues.

ADDITIONAL SPECIMENS EXAMINED: **ESTONIA**, SAARE, **Saaremaa**, near Viidu, on rotten wood, 10.10.2010, Vello Liiv (TUF106979; UNITE UDB015277); on deciduous twigs, 28.09.2012, Vello Liiv (TUF118453; UNITE UDB018190); **PÄRNU**, **Pärnumaa**, Nigula mire, swamp forest, on fallen leaves of *Populus tremula*, 03.10.2011, Vello Liiv (TUF118289; UNITE UDB015455). **FINLAND**, INARIN LAPPI, Utsjoki, Kenesjärvi, 14.09.1972, Martti Ohenoja (OULU-F-16606; UNITE UDB07672483); **PERÄ-POHJANMAA**, **Lapland**, Tornio, Kalkkima SE, near Alatolo farm, S side of the road, deciduous forest (*Alnus*), 16.09.1986, Esteri Ohenoja, Tuula Vuorinen (OULU-F-16597; UNITE UDB07672480); **SOMPION LAPPI**, Pelkosenniemi, Suvanto NW, Niskakorpi, Niskaojan varsi, N-side of road, 11.09.1985, Esteri Ohenoja (OULU-F-16603; UNITE UDB07672482); Pelkosenniemi, Siulioaapa NE, 25.08.1994, Ulla Nummela-Salo, Pertti Salo (OULU-F-24076; UNITE UDB07672485). **NORWAY**, TROMS, Lullesletta, rich deciduous forest along a brook, 19.08.1992, Esteri Ohenoja OULU-F-21543; UNITE UDB07672484). **SWEDEN**, NORRBOTTEN, **Piteå**, Mjöviksmoåsen, 10.1982, Brigitta Öster (UPS-F-740369; UNITE UDB07672488).

ECOLOGY: saprobic on same year's fallen deciduous leaves, most commonly *Populus tremula*, or deciduous litter.

HABITAT: deciduous and mixed woods.

PHENOLOGY: September–October; neotype appeared after first night frost.

DISTRIBUTION: So far confirmed from the Northern Hemisphere, both sides of both North America and Eurasia.

COMMENT. The macroscopic description of *O. umbellifera* is based primarily on the neotype specimen. To spare type material, microscopic observations were augmented by or based entirely on sequence-confirmed conspecific material. A fuller species concept is expected to evolve as *Owingsia* and its species get resolved taxonomically.

Search for a new name for AM-MIN

We began this quest by reviewing descriptions of AM-MIN culled from the cited major workers and those they have quoted, MycoBank and Species Fungorum, appropriate texts, and other sources. FIGURE 7 is a composite plate of some illustrated candidates for AM-MIN from the past, many used in past typification attempts, labelled with year of publication, author, and binomial (where available), all cited in the legend. The plate is arranged in rows to facilitate the discussion around the search for the optimal name. Note that the pleomorphic appearance of the species on this plate resembles that seen on modern photos of AM-MIN (FIG. 1).

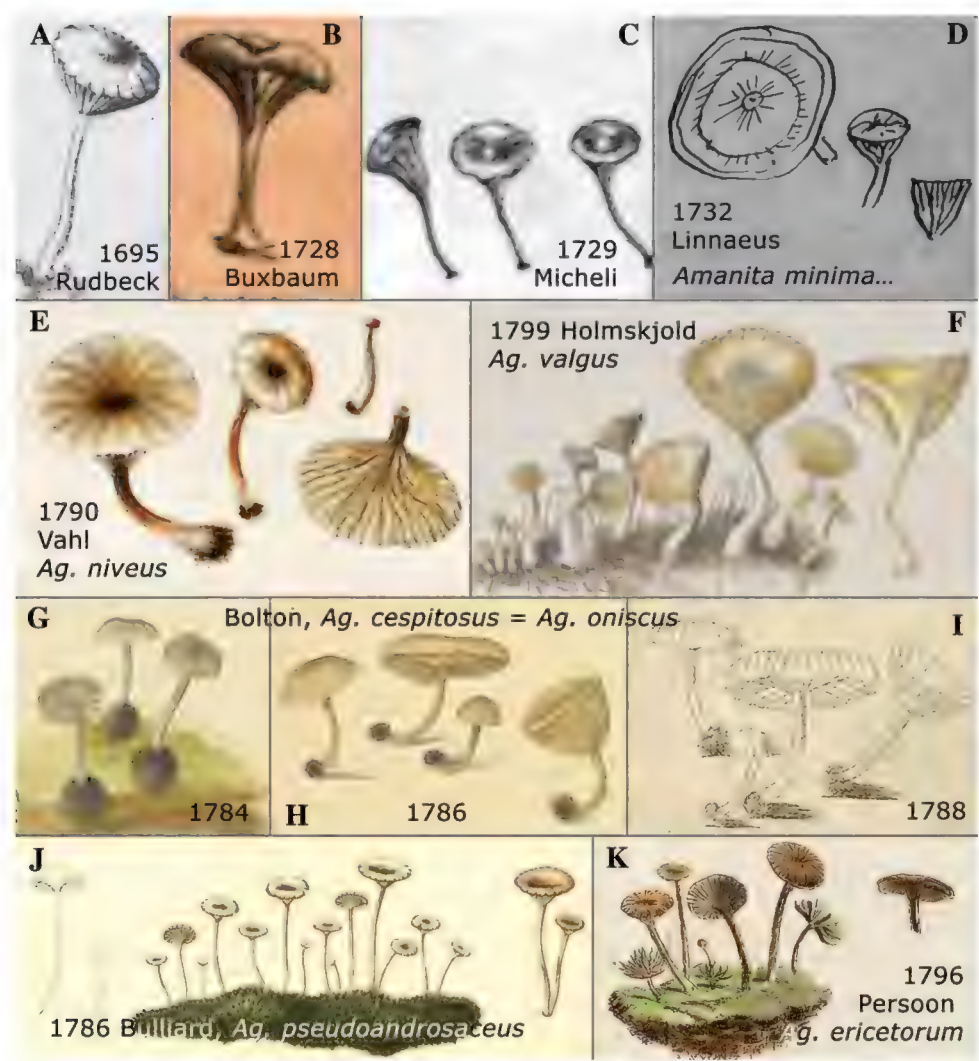


FIG. 7. Composite plate of some real or potential AM-MIN synonyms. Morphological variation akin to that seen on FIG. 1. A. Illustration by Rudbeck (Anfält 1987) of a specimen resembling AM-MIN—same as FIG. 2E, above; no name or description given; B. Illustration by Buxbaum (1728) of a specimen resembling AM-MIN, phrase name given; C. Illustration by Micheli (1729) of a specimen resembling AM-MIN—same as FIG. 2C, above; phrase name given; D. Illustration by Linnaeus (Fries 1913) of a specimen resembling AM-MIN—same as FIG. 2E, above; phrase name given; E. Protologue illustration by Vahl (1790) of *Agaricus niveus*; F. Protologue illustration by Holmskjold (1799) of *Agaricus valgus*; G. Prepublication illustration by Bolton (1784) of *Agaricus cespitosus*, also labelled *Agaricus umbelliferus*; H. Prepublication illustration by Bolton (1786) of *Agaricus*

cespitosus, selected as lectotype for *Agaricus cespitosus* by Voitek (2022); I. Protologue illustration by Bolton (1788) of *Agaricus cespitosus*, selected as lectotype for *Agaricus oniscus* by Voitek (2022); J. Protologue illustration by Bulliard (1786) of *Agaricus pseudoandrosaceus*, the middle group on a moss cushion selected as lectotype for *Agaricus ericetorum* by Redhead & Kuyper (1987); K. Protologue illustration by Persoon (1796) of *Agaricus ericetorum*.

The upper row, FIGS 7A–D, predate the use of binomial names; FIG. 7A was drawn but not named or described, and FIGS 7B–D were identified by a phrase name. All appeared before 1753, i.e., before the starting-point of valid fungal nomenclature (Art. F.1). Hence, even had they been named, the names would be considered unavailable.

The second row of FIG. 7 shows two taxa with a striking resemblance to AM-MIN. FIGURE 7E, *A. niveus*, is an illegitimate name because the epithet was already in use in *Agaricus*, and is thus not available. FIGURE 7F, *A. valgus*, is unsanctioned, and, therefore, plays no role in the nomenclature of AM-MIN, so long as a fitting sanctioned name is available.

The third row, FIGS 7E–G, show three illustrations by Bolton of *Agaricus cespitosus*, minimally adapted for space. FIGURES 7G & H come from two volumes in a prepublication folio manuscript, handwritten and hand-painted (Bolton 1784, 1786), each obviously based on a different collection. FIG. 7I shows Bolton's definitive copper plate, used to illustrate his formal printed description of the species (Bolton 1788), obviously based on FIG. 7H. These illustrations were used by Voitek (2022) in a detailed discussion of the synonymy of *A. cespitosus* with *A. oniscus* Fr. nom. sanct., and their conspecificity with AM-MIN. Namely, 30 years after Bolton described AM-MIN with the name *A. cespitosus*, Fries (1818) described *A. oniscus*, stating that this new name was to exclude the name *A. cespitosus*. Ordinarily a new name for a legitimate earlier name would be deemed illegitimate as superfluous, but Fries described *A. oniscus* again in his *Systema Mycologicum* (Fries 1821), giving *A. oniscus* sanctioned priority over *A. cespitosus*. Their synonymy was formalized by declaring the illustration shown in FIG. 7H as lectotype for *A. cespitosus* and FIG. 7I as lectotype for *A. oniscus* (Voitek 2022). Because FIG. 7H was used to make FIG. 7I, the species are homotypic. [We note that due to a typographical error, Voitek (2022) listed the date of publication of Bolton's painting chosen for lectotypification of *A. cespitosus* as 1784, instead of 1786. The correct year appears elsewhere in Voitek's article, and both the description of the image and the citation of source are clear, making the required correction patent.] Although Fries declared that the sanctioned *A. oniscus* was to replace all synonyms (i.e., past, present, and future) for *A. cespitosus*, it takes effect on the

publication date of its protologue, 1818. This gives any sanctioned name for AM-MIN published before 1818 priority over *A. oniscus*.

The fourth row, FIGS 7J & K, are protologue illustrations for the earliest description of AM-MIN, *A. pseudoandrosaceus* Bull. (Bulliard 1786), and its declared synonym, *A. ericetorum* Pers, described ten years later (Persoon 1796). Again, ordinarily this later synonym would be considered a superfluous name, but when Fries described the taxon in his 1821 *Systema*, *A. ericetorum* became sanctioned, taking precedence over Bulliard's name. This ascension to precedence suffered a little transient hiccup because earlier versions of the Code did not extend sanction to names of lichenized fungi. Therefore, when lichenized basidiomycetes were recognized, and AM-MIN considered one of them, Persoon's name was considered superfluous. Only after the Code extended the same sanctioning rules to names of lichenized fungi, did *A. ericetorum* gain its priority over *A. pseudoandrosaceus*. The effective publication of this sanctioned name was 1796, 22 years before the sanctioned *A. oniscus*, giving *A. ericetorum* priority. Both *A. pseudoandrosaceus* and *A. ericetorum* were lectotypified (Redhead & Kuyper 1987) with the central light-coloured basidiomata on a moss cushion of FIG. 7J, Bulliard's protologue illustration, making them homotypic, thus formalizing Persoon's intended synonymy. One earlier lectotypification (Singer 1961) with a collection made by Persoon was rejected by Redhead & Kuyper because it had not been seen by Bulliard (i.e., could not be part of Bulliard's original material), and was undated, thus lacking evidence that it was part of Persoon's original material. Hence, Redhead & Kuyper's lectotypification is the earliest, and should be followed, according to the Code, now that *A. umbellifer* has been recombined in accordance with its protologue as *Owingsia umbellifera*. In other words, the sanctioned *A. ericetorum* regains its priority (Arts 11.4, F.3) as the basionym for AM-MIN. So long as *A. pseudoandrosaceus* and *A. ericetorum* are homotypic, attempts to treat them as separate taxa are erroneous (e.g. Singer 1961, Moser 1983), as is the combination of *A. pseudoandrosaceus* to *Mycena* (Bi & al. 1987). Another typification of *A. ericetorum* that should be revised is the epitype designated by Jørgensen & Ryman (1994): specimen 1753 from Fungi Exsiccati Suecici. In the belief that *A. ericetorum* and *A. umbellifer* were synonymous, Jørgensen & Ryman declared it epitype for both. As we see, these names now represent two different species, leaving this typification without standing (Arts 9.18 and 9.20). This paragraph is but a condensed review of a very complex nomenclatural story involving these taxa. Much more detail is

available in Redhead & Kuyper (1987), Redhead & al. (2002), and the many references cited by these authors.

In short, Redhead & Kuyper (1987) have already identified an appropriate name for AM-MIN with a lectotypification, subsequently rejected by Redhead & al. (2002). Should we wish to reconsider it, our task is to ensure that this earliest available name for AM-MIN still remains appropriate and can be reinstated. Persoon cited *A. pseudoandrosaceus* as a synonym, but there must be no conflict between the two protologues, including all associated original material, for his opinion to be valid. There is an obvious colour difference between the two protologue illustrations, Persoon's being much darker than Bulliard's. This discrepancy disappears in their protologue descriptions, making both compatible with each other and with AM-MIN. Bulliard described *A. pseudoandrosaceus* as white to ash grey (gris cendré), occasionally yellowish white. Persoon described *A. ericetorum* as light grey (fragile griseo), and quoted Sibthorpe's (1794) description, lightly dusky (subfusco). The varying references to light grey are compatible with a moist translucent whitish cap, a common appearance of AM-MIN—see FIG. 7G, and a detailed discussion with contemporary photos of this by Voitek (2022). Persoon described the base of the stipe as white, covered with tomentum, and the lamellae as whitish. These descriptions are not congruent with the dark brown basidiomata of Persoon's illustration, suggesting technical problems with rendering accurate colour. Although Persoon did not comment about the colour of his illustration (he may not have seen it at the time of writing), he did mention that the artist had failed to illustrate the shape of the gills adequately, raising some questions about the accuracy of the illustration even before it was painted. We polled five arctic-alpine experts familiar with AM-MIN (Torbjørn Borgen, Jozsef Geml, Gro Gulden, Pierre-Arthur Moreau, Anna Ronikier) about the compatibility of Persoon's illustration with AM-MIN, and not surprisingly, all found the basidiomata dark. Two thought that it was incompatible, without qualification, one specified that the image would be very accurate if it were of lighter colour, and two had no hesitation to accept them as is: one of them volunteered that AM-MIN is so pleomorphic that its spectrum even encompasses the basidiomata on Persoon's image, while the other stated that the green ground cover almost certainly represented a botryoid lichen thallus, and the basidiomal colour should be disregarded entirely, because of the known inaccuracy of hand-painting. Thus, the only problem with the image identified was dark colour, which found no support in the descriptions, and seems best attributed to a

technical artifact. We note that just as Redhead & Kuyper selected only light basidiomata for typification, when choosing a lectotype for *A. oniscus*, Voitk (2022), on encountering a wide variation in colour of hand-painting the same engraving of *A. cespitosus*, specified an unpainted one for typification. Other examples abound. For instance, images of the white *A. porcellaneus* Schaeff. published by Schaeffer (1774), subsequently appear from light to very dark brown in different issues of Bulliard's *Herbier de la France*, vol 1 (Bulliard 1780).

Our conclusion was that the most likely species intended by both Bulliard and Persoon was AM-MIN, making them synonyms. Although other explanations are possible, support for them seems considerably more tenuous. Therefore, we have no hesitation rejecting the rejection of Redhead & al. of Redhead & Kuyper's lectotypification of both *A. pseudoandrosaceus* and *A. ericetorum*—in other words, reinstating Redhead & Kuyper's lectotypification of both *A. pseudoandrosaceus* and *A. ericetorum* with Bulliard's protologue illustration of *A. pseudoandrosaceus*.

Taxonomy

Lichenomphalia ericetorum (Pers.) Voitk, Thorn & I. Saar, **comb. nov.** FIGS 1, 8
MB 845595

≡ *Agaricus ericetorum* Pers., *Observ. Mycol.* 1: 50. 1796 (nom. sanct., Fries, *Syst. Mycol.* 1: 165. 1821)

≡ *Agaricus pseudoandrosaceus* Bull., *Herb. France* 6: tab. 276. 1786.

TYPE: **Holotype**: none designated or preserved. **Lectotype** [MBT593068, Redhead & Kuyper 1987], Bulliard tab. 176, 1786, *Agaricus pseudoandrosaceus*. *Herbier de la France* 6: tab. 276. **Epitype** [here designated, MBT10013917], Estonia Tartumaa, Järvselja, 58.2668°N 27.3179°E, 25.08.2016, V. Liiv (TUF120612).

= *Agaricus oniscus* Fr., *Observ. Mycol.* 2: 209. 1818 (nom. sanct., Fries, *Syst. Mycol.* 1: 172. 1821)

≡ *Agaricus cespitosus* Bolton, *Hist. Fung. Halifax* 1: 41, pl. XLI, fig. C. 1788.

MISAPPLICATIONS:

≠ *Agaricus umbellifer* L., *Sp. Pl.* 2: 1175. 1753.

≡ *Amanita umbellifera* (L.) Roussel, *Fl. Calvados*: 34. 1796.

≡ *Merulius umbellifer* (L.) With., *Arr. Brit. Pl.*, Edn 3, 4: 147. 1796.

≡ *Omphalia umbellifera* (L.) P. Kumm., *Führ. Pilzk.*: 107. 1871.

≡ *Omphalina umbellifera* (L.) Quél., *Enchir. Fung.*: 44. 1886.

≡ *Clitocybe umbellifera* (L.) H.E. Bigelow, *Can. J. Bot.* 37: 773. 1959.

≡ *Lichenomphalia umbellifera* (L.) Redhead & al., *Mycotaxon* 83: 38. 2002.

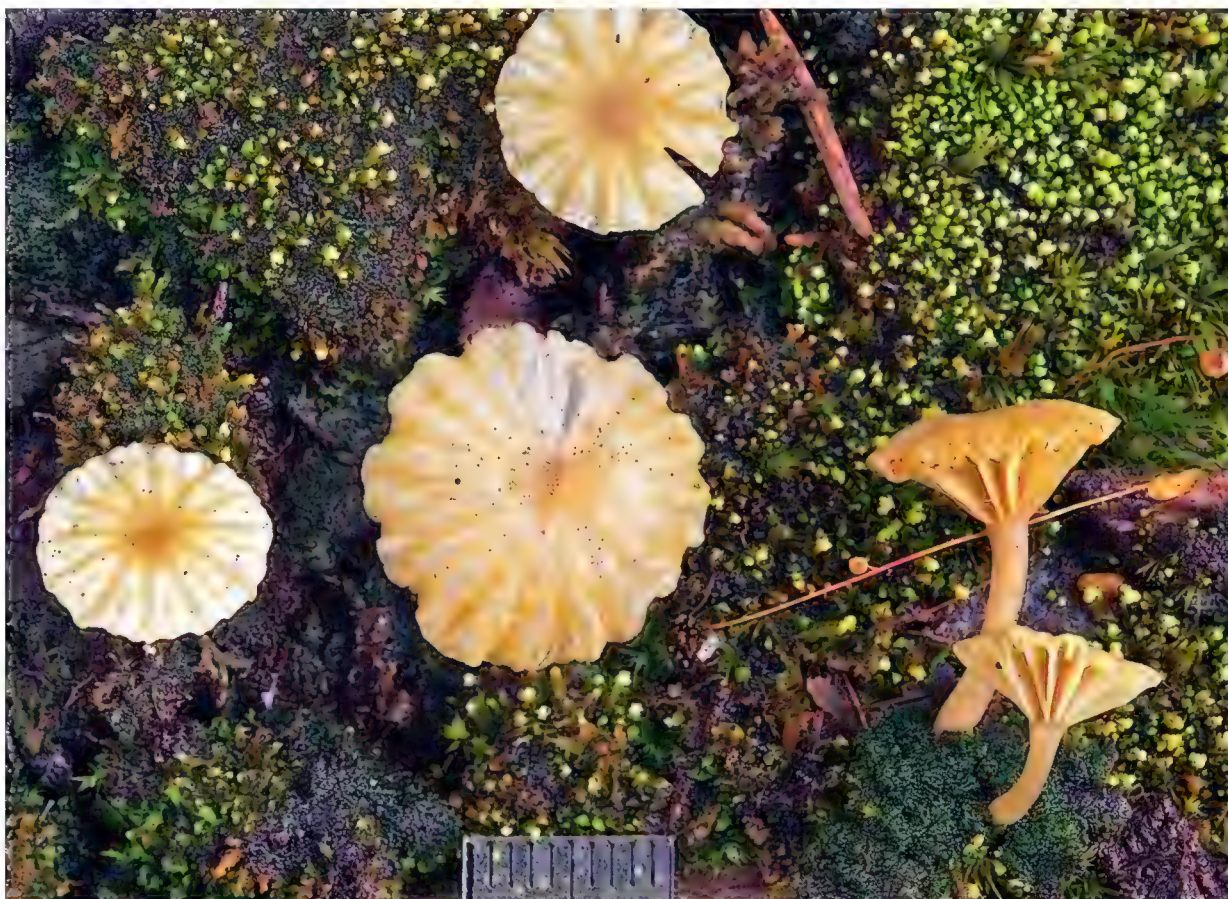


FIG. 8. Epitype of *Lichenomphalia ericetorum* (TUF120612) in situ. Photo: Vello Liiv.

CAPSULAR EPITYPE DESCRIPTION (FIG. 8)

MACROSCOPIC: Basidiomata omphalinoid. Pileus up to 20 mm, low convex to plane, centre often umbilicate, smooth, margin crenulate, translucently striate, pale yellow. Lamellae deeply decurrent, sometimes forked, distant, concolorous with pileus or paler. Stipe 10–20 × 1–2 mm, smooth, dry, yellowish.

MICROSCOPIC: Basidiospores 7.5–12 × (4.8–)5.3–8.8 µm, mean 9.9 × 6.8 8 ± 1.4 µm, Q = 1.3–1.6, mean 1.4 ± 0.1; hyaline, inamyloid, broadly ellipsoid to ellipsoid. Basidia 30–32 × 9–11 mm, 4-spored. Cystidia and clamp connections absent.

NOTE: FIG. 1 and its legend discussion give an overview of the pleomorphic spectrum of the species.

Discussion

Completion of this quest was only made possible by unprecedented good fortune. Our first anticipated impediment was the nature of early species descriptions: often very brief, somewhat vague, lacking important information, inconsistent, and seemingly based on what are often considered several species.

With respect to *A. umbellifer*, Linnaeus surprised us with a consistent cluster of solid characters that formed a very clear picture of the species he had in mind. A robust species concept makes comparison for fit to a known species much easier, but this particular step of the enquiry was greatly aided by Redhead & Kuyper (1987), who had already documented the major conflicts arising from trying to apply *A. umbellifer* to AM-MIN.

The hubris of requiring that we find an unequivocal fit for *A. umbellifer* was not lost on us, and we retained healthy skepticism about our ability to meet it. We set this condition knowingly at the outset, in the belief that nomenclatural stability would be served only if *Agaricus umbellifer* were securely fixed by concinnous typification. A commodious match for the epithet would: a) be a solid test of whatever species concept we could develop from Linnaeus's writings; b) avoid orphaning a name in use for over a quarter millennium; and c) justify the search for a more fitting name for AM-MIN. Success would require familiarity with Lapland mycota, something not possible from a desk, bookshelf, or armchair.

This step was realized, against our own expectations, partly thanks to the limpid picture painted by Linnaeus's descriptions. Just as Linnaeus immediately recognized the species on Öland, some nine years after seeing it in Lapland, the senior author, AV, once armed with a clear vision of Linnaeus's concept and its Lapland location, immediately recalled a similar species he had encountered in Lapland 14 years earlier. This find was not the result of foresight or clever experimental design, but mere fortuitous happenstance. Because one of his sons lived several years in Norwegian Lapland, AV had made multiple visits to the area, exploring the region between Finnsnes and Nordkapp, east to nearby Finland. In addition to the iconic AM-MIN, documented by both Rudbeck and Linnaeus, he encountered several species typical of the habitat, some of which have been reported elsewhere [*Gomphidius roseus* (Fr.) Oudem. (Aime & Voitk 2014); *Cantharellus cibarius* Fr. (Thorn & al. 2017); *Chromosera lilacina* (P. Karst.) Vizzini & Ercole (Voitk & Voitk 2020); *Arrhenia philonotis* (Lasch) Redhead & al. (Voitk & al. 2022)]. Encountering *O. umbellifera* (FIG. 3) in 2006 made it clear why it is not collected more frequently. For over a week AV had taken the same forest path daily to explore the barren higher land around the tree line, without seeing this species. One morning, after the first night frost, large numbers became evident on fallen leaves along the forest trail, where none had been noted the day before. The following day, when the photo for FIG. 3A was taken, very few were left, and on the third day it was difficult to find any sign of their passing. Scopoli (1772) confirmed that this is not a

chance observation, noting “brevis vita” as one of characters of *A. umbellifer*. In other words, even if the species is common and ubiquitous, it can easily escape detection because of its unison fruiting within a very narrow timespan and its capriciously ephemeral basidiomata.

Finding an epiphyllic species on fallen leaves of *P. tremula*, appropriately another Linnaeus species, around 70°N may seem unexpected, but Lapland is warmed by the tail end of the Gulf Stream (Voitk 2021), enabling substantial coniferous and deciduous forests to thrive north of the Arctic Circle. As glaciation receded, the psychrophilic *P. tremula* passed through Fennoscandia and the Baltic Sea islands to traverse Lapland, and reach Murmansk and beyond. With it came *O. umbellifera*, served up to us by serendipity on the aspen-lined Lapland trail. This species, confirmed to be prevalent in Lapland by our sequences (FIG. 6), accommodates Linnaeus’s protologue for *A. umbellifer* better than any earlier attempt, reconciling even the flat cap that had remained a problem in the past. Applying *A. umbellifer* to a fitting species permits Fries’s apportionment of Micheli’s epiphyllic fungus to remain intact, also a more fitting result.

In their deliberations, Redhead and colleagues suspected that, just as Linnaeus’s descriptions of *A. umbellifer*, descriptions of *A. pseudoandrosaceus* and *A. ericetorum* also incorporated elements from more than one species. Recent technological advances, like molecular studies, confirm this as very likely: the ability to identify evolutionary pathways has uncovered many complexes of cryptic species hiding under one name. Some of the species in *Owingsia*, all identified as *Marasmius epiphyllus*, may prove to be one such example. The lack of unanimity among our expert panel confirms that Bulliard’s and Persoon’s illustrations are a bit shy of ideal, even if they lack such major conflicts like long vs normal stipe and epiphyllic vs non-epiphyllic ecology. Many, if not most old descriptions can be assumed to contain elements of more than one species, which becomes a general problem for future nomenclatural and taxonomic work. If the conflict trigger becomes too sensitive, options may be to disregard all old descriptions as inaccurate, vague, or otherwise imperfect, and treat each species as new. Alternately, all such questions may be sent to binding resolution by motions to conserve one name against another. Neither approach seems attractive. Detailed review of the original material convinced us that, despite some slight aberrations possibly due to technical factors and possibly to unpreventable inclusion of similar species, AM-MIN was by far the most likely species intended by *A. pseudoandrosaceus* and *A. ericetorum*.

Were we to reject the synonymy of *A. ericetorum* and *A. pseudoandrosaceus*, the earliest valid names for AM-MIN would become *A. cespitosus*, with a closer fit to AM-MIN than has *A. ericetorum*, and replaced by the sanctioned *A. oniscus*, whose synonymy with *A. cespitosus* seems beyond challenge according to current rules of nomenclature. However, such rejection would be based on very small inconsistencies, difficult to defend—a weak foundation inviting future challenges. Nomenclature, lacking an inherent need for change, should strive to follow the “one fungus = one name” (Taylor 2011) principle that makes infungible fungal epithets a marked improvement on common names. However, we lack the enthusiasm of some onomasts for nomenclatural stability at all cost, and believe that there should be no hesitation to correct application of names producing serious conflict with the original protologue material. Stability in such considerations should not confuse “established custom” with personal preference, which only moves instability to the future. In these times of great phylogenetic discovery, names change almost daily. Correction of a few discordant nomenclatural misapplications accounts for a negligible proportion of these changes, almost all of which come from changed taxonomic concepts. Stability in taxonomy is an unrealistic and unattainable goal, because taxonomy is evidence-based ranking, inherently changing as new knowledge accrues.

An interesting observation during this work was that reassessment of how we interpret citations may be helpful; automatically assigning synonymy to every citation may not reflect the authors’ intent. Consider that Linnaeus stated five times that the pileus of *A. umbellifer* is flat, yet cited illustrations of one species with a hemispherical and another with a subconic pileus. To maintain that Linnaeus cited these as synonyms, something he did not claim, presupposes that either he did not know the meaning of the “flat”, or was blind—yet it has been done. [In contrast, consider that although Fries stated in no uncertain terms that he introduced *A. oniscus* specifically as a synonym to exclude *A. cespitosus*, many workers elected to ignore Fries’s stated intent, and applied *A. oniscus* to morphologically different taxa, totally unrelated to the original material supporting the epithet (Voitk 2022).]

Fries’s handling of *A. umbellifer* provides a further opportunity to examine interpretation of citations. Fries (1825) first mentioned *A. umbellifer* in a review of the flora around his home, Femsjö, stating that Linnaeus’s synonym was surely restored, thus emphasizing that the species concept under discussion is that of Linnaeus. Fries did not describe the species, but instead cited Pollich (1777), saying the latter provided a good description of it. Indeed, Pollich cited three of Linnaeus’s descriptions as well as the Micheli description cited by Linnaeus,

discussed above, and another description by Scopoli (1772). All described a small white long-stemmed basidioma, to which Pollich added a description of the pileus (white, convex, becoming plane) and lamellae (white, initially arising evenly, then descending slightly to become subdecurrent at the stem). Pollich's description augmented by the descriptions he cited, is congruent with the species concept of Linnaeus and matches *O. umbellifera*. Fries next sanctioned *Agaricus umbellifer*. Again, Fries did not describe the taxon himself. The heading, "*A. umbelliferus* Linn.," is a de facto citation of Linnaeus's description (Linnaeus 1753), to which Fries added a citation of his first treatment of the name, described above, which provided various citations of descriptions fitting that of Linnaeus. Thereafter followed three citations of works applying *A. umbellifer* to a short-stemmed (stipite brevi) species: Wahlenberg (1826), Sommerfeldt (1826), and Fries's treatment of *A. ericetorum* (Fries 1821).

It is highly unlikely that anyone, let alone the father of Friesian taxonomy, would proffer species with such discordant characters as long and short stems as conspecific. The only logical conclusion we could draw is that the reason to mention treatments of a short-stemmed species as *A. umbellifer* was an attempt to alert the reader to some recent misapplications of the Linnaean name. We know that Fries had no difficulty indicating synonymy, when such was his intent; perhaps the reason he did not declare the last three citations as conspecific was that he did not believe they were. That this was Fries's intent finds strong support from his citation of his own description of *A. ericetorum* (Fries 1821). He very specifically indicated that he did **not** cite it as a synonym, by preceding the citation with "V." (videre = see, view), an invitation to the reader to view (in the sense of compare and contrast) the description to judge its aptness. Surely, he was not inviting the reader to compare *A. ericetorum* to the *A. umbellifer* of Linnaeus? He knew these were different species characterized by markedly different sized stipes and markedly different substrate preferences. Rather, he invited a comparison of *A. ericetorum* to the species to which both Wahlenberg and Sommerfeldt had misapplied the epithet *umbellifer*, an obvious suggestion that *A. ericetorum* may be a better fit for those species than (the misapplied) *A. umbellifer*. Therefore, it is not surprising to learn that the descriptions of Wahlenberg and Sommerfeldt do resemble *A. ericetorum* far better than *A. umbellifer*. Failure to understand this has caused some regrettable confusion that Fries sought to synonymize *A. ericetorum* with *A. umbellifer*.

We dealt with two species concepts described over 200 years ago, both interpreted and reinterpreted with much passionate debate over the years. The original names of both have been misapplied to other species, and both species

have had other names misapplied to them. Whether achieved by luck or design, finding names to apply to both species that fit the original material without conflict, reflect their authors' intent, and observe current rules of nomenclature is gratifying.

Epilogue

The Preamble to the Code states, "The object of the rules is to put the nomenclature of the past into order and to provide for that of the future ... The only proper [reason] for changing a name [is] ... a more profound knowledge of the facts resulting from adequate taxonomic study ..." We believe our solution embodies this object, while settling a longstanding problem. The major attraction of this solution is its pleasing concinnity: the application of *A. umbellifer* will be the first since Linnaeus's description that will fit his concept without conflict, and the familiar *A. ericetorum* will be reinstated, hopefully to continue the stability it enjoyed earlier. Names fitting with their original material without conflict are unlikely to need change, ensuring future stability in return for minimal transient discomfort. We wish to leave stable names to our colleagues of tomorrow, rather than ask them to accept ill-fitting names because for a brief period in the long history of these names we may have become comfortably accustomed to one version of their misapplication.

Acknowledgments

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Moreau (Université de Lille, France), as formal reviewers, made major contributions to a revised and improved content; the Editor-in-Chief, Lorelei Norvell, is thanked for pertinent suggestions, as well as help with buffing textual asperity to produce a more accurate and readable final product; an especial thanks is owed to the Nomenclatural Editor, Shaun Pennycook, who worked beyond reasonable editorial limits to minimize the authors' deficiency in this area. This is the second nomenclatural study prompted by a review of sphagnicolous arrhenias (Voitk & al. 2022), and understandably, in addition to the assistance acknowledged here, we are indebted to all whose efforts were gratefully documented in the original study and its first nomenclatural derivative (Voitk 2022), which spawned the current investigation.

Literature cited

- Aime C, Voitk A. 2014. *Gomphidius* in Newfoundland and Labrador with a redescription of *Gomphidius borealis*. *Omphalina* 5(3): 3–10.
- Anfält T. 1987. Rudbeck's (1695) *Iter Lapponicum*—skissboken från resan till Lappland. Coeckelberghs, Stockholm.
- Antonín V, Noordeloos N. 1993. A monograph of *Marasmius*, *Collybia* and related genera in Europe. Part 1: *Marasmius*, *Setulipes*, and *Marasmiellus*. *Libri Botanici* 8. 229 p.
- Antonín V, Vašutová M, Urban A. 2010. A molecularly supported concept of *Marasmius epiphyllus* (*Basidiomycetes*, *Physalacriaceae*). *Cryptogamie, Mycologie* 31: 355–362.
- Bi Z-S, Li T-H & Zheng G-Y. 1987. Taxonomic studies on *Mycena* from Guang-Dong Province of China. *Acta Mycologica Sinica* 6(1): 8–14.
- Binder M, Hibbett DS, Wang Z, Farnham WF. 2006. Evolutionary relationships of *Mycaureola dilseae* (*Agaricales*), a basidiomycete pathogen of a subtidal rhodophyte. *American Journal of Botany* 93: 547–556. <https://doi.org/10.3732/ajb.93.4.547>
- Bolton J. 1784. *Icones fungorum circa Halifax sponte nascentium*, vol. 1. Publ. by author, Halifax. <https://doi.org/10.5962/bhl.title.160058>
- Bolton J. 1786. *Icones fungorum circa Halifax sponte nascentium*, vol. 3. Publ. by author, Halifax. <https://doi.org/10.5962/bhl.title.160058>
- Bolton J. 1788. *An history of fungusses growing about Halifax*, vol. 1. Publ. by author, Halifax. 44 p. <https://doi.org/10.5962/bhl.title.5394>
- Bulliard P. 1780. *Agaricus porcellaneus* Schaeffer. *Herbier de la France* 1: tab. 16. Publ. by author, Paris.
- Bulliard P. 1786. *Agaricus pseudo-androsaceus*. *Herbier de la France* 6: tab. 276. Publ. by author, Paris.
- Buxbaum JC. 1728. *Centuria II. Typographiae Academiae, Petropoli*.
- Buxbaum JC. 1733. *Centuria IV. Typographiae Academiae, Petropoli*.
- Desjardin DE. 1989. The genus *Marasmius* from the southern Appalachian Mountains (PhD thesis). University of Tennessee.
- Dillenius JJ. 1719. *Catalogus plantarum sponte circa Gissam nascentium*. Joh. Maximilian à Sande, Francofurti.
- Fries EM. 1818. *Observationes mycologicae*, vol. 2. Bonnier, Kjøbenhavn. 376 p. <https://doi.org/10.5962/bhl.title.112534>
- Fries EM. 1821. *Systema mycologicum*, vol. 1. Lund. 520 p.
- Fries EM. 1825. *Stirpium agri femsionensis*. *Typographia Academica*, Lund.
- Fries EM. 1828. *Elenchus fungorum*, vol. 1. Mauritius, Greifswald. 238 p.

- Fries TM. 1913. Skrifter af Carl von Linné, vol. 5: Iter Lapponicus. Swedish Royal Academy of Science, Uppsala.
- Geml J, Kauff F, Brochmann C, Lutzoni F, Laursen GA, Redhead SA, Taylor DL. 2012. Frequent circumarctic and transequatorial dispersals in the lichenized agaric genus *Lichenomphalia* (*Hygrophoraceae*, *Basidiomycota*). *Fungal Biology* 116: 388–400. <https://doi.org/10.1016/j.funbio.2011.12.009>
- Greuter W, McNeill J, Barrie FR, Burdet H-M, Demoulin V, Filgueiras TS & al. 2000. International Code of Botanical Nomenclature (St Louis Code). Adopted by the sixteenth International Botanical Congress St. Louis, Missouri, July–August 1999. *Regnum Vegetabile* 138. Koeltz Scientific Books, Königstein. 474 pp.
- Haller A von. 1742. *Enumeratio methodica stripium Helvetiae indiginarum*, vol. 1. Officina Academica Abrami Vanderhoek, Göttingen.
- Holmskjöld T. 1799. *Agaricus valgus*. *Beata Ruris Otia Fungis Danicis* 2: 62, tab. 34.
- Jenkinson TS, Perry BA, Schaefer RE, Desjardin DE. 2014. *Cryptomarasmius* gen. nov. established in the *Physalacriaceae* to accommodate members of *Marasmius* section *Hygrometrici*. *Mycologia* 106: 86–94. <https://doi.org/10.3852/11-309>
- Jørgensen PM, Ryman S. 1989. Proposal to Conserve *Omphalina* Quélet over *Phytoconis* Bory and *Botrydina* Brébisson (*Basidiomycetes*). *Taxon* 38: 305–308. <https://doi.org/10.2307/1220869>
- Jørgensen PM, Ryman S. 1994. On the typification of *Omphalina umbellifera* (L. : Fr.) Quél. (*Fungi*, *Agaricales*). *Taxon* 43: 253–255. <https://doi.org/10.2307/1222884>
- Kim MS, Klopfenstein NB, Hanna JW, McDonald GI. 2006. Characterization of North American *Armillaria* species: genetic relationships determined by ribosomal DNA sequences and AFLP markers. *Forest Pathology* 36: 145–164. <https://doi.org/10.1111/j.1439-0329.2006.00441.x>
- Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor A, Bahram M, Bates S & al. 2013. Towards a unified paradigm for sequence-based identification of *Fungi*. *Molecular Ecology* 22: 5271–5277. <https://doi.org/10.1111/mec.12481>
- Kühner R. 1933. Études sur le genre *Marasmius*. *Le Botaniste* 25: 57–115.
- Linnaeus C. 1732. *Iter Lapponicum*. [See Fries TM. 1913, above.]
- Linnaeus C. 1737. *Flora Lapponica*. Swedish Royal Academy of Science. Amsterdam.
- Linnaeus C. 1741. *Iter Celandicum*. Handwritten journal
- Linnaeus C. 1745. *Flora Suecica*, ed. 1. Laurentii Salvii, Stockholm.
- Linnaeus C. 1753. *Species Plantarum*, vol. 2. Laurentii Salvii, Stockholm.
- Linnaeus C. 1755. *Flora Suecica*, ed. 2. Laurentii Salvii, Stockholm.
- Lange M. 1955. Den botaniske ekspedition til Vestgrønland 1946. *Meddelerser om Grønland* 147: 25.
- Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W & al. 2006. Major clades of *Agaricales*: a multilocus phylogenetic overview. *Mycologia* 98: 982–995. <https://doi.org/10.1080/15572536.2006.11832627>
- Micheli PA. 1729. *Nova plantarum genera*: 166, tab. 80, fig. 11. Bernardi Paperinii, Florentiae.
- Moser M. 1983. *Keys to Agarics and Boleti*. (Polyporales, Boletales, Agaricales, Russulales). 4th ed. Roger Phillips, London. 535 p.
- Nilsson Ö. 1987. *Skissbokens botaniska bilder*. In: Rudbeck O, *Iter Lapponicum II*. Stockholm.
- Nilsson RH, Larsson K-H, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D & al. 2019. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Research* 47(D1): D259–D264 <https://doi.org/10.1093/nar/gky1022>

- Owings P. 1997. Evolutionary relationships within the genus *Marasmius* inferred by morphological and nrDNA sequence comparisons (MSc thesis). San Francisco State University, San Francisco.
- Owings P, Desjardin DE. 1997. A molecular phylogeny of *Marasmius* and selected segregate genera. *Inoculum* 48: 29–30.
- Persoon CH. 1796. *Observationes mycologicae* 1: tab. IV, fig. 12. Petrum Phillippum Wolf, Lipsiae.
- Petersen RH, Hughes KW. 2010. The *Xerula/ Oudemansiella* complex (Agaricales). *Beihefte zur Nova Hedwigia* 137. 625 p.
- Pinto-Guillaume E. 2017. Sami people: natural resources and climate change. IAIA17 Conference Proceedings, 37th Annual conference of the International Association for Impact Assessment, April, 2017, Montréal.
- Pollich JA. 1777. *Historia plantarum in Palatinatu electorali*, vol 3. C.F. Schwan, Mannheim. 320 p.
- Ray J. 1724. *Synopsis methodica stirpium brittannicarum*, ed. 3. Regiae Societatis Typographorum, London.
- Redhead SA, Kuyper TW. 1987. Lichenized agarics: taxonomic and nomenclatural riddles. *Arctic and Alpine Mycology* II: 319–348. https://doi.org/10.1007/978-1-4757-1939-0_21
- Redhead SA, Weresub LK. 1978. On *Omphalia* and *Omphalina*. *Mycologia* 70: 556–568. <https://doi.org/10.2307/3759393>
- Redhead SA, Lutzoni F, Moncalvo J-M, Vilgalys R. 2002. Phylogeny of agarics: partial systematics solutions for core omphalinoid genera in the Agaricales (*Euagarics*). *Mycotaxon* 83: 19–57.
- Ronikier M, Ronikier A. 2011. *Rhizomarasmius epidryas* (*Physalacriaceae*): phylogenetic placement of an arctic-alpine fungus with obligate saprobic affinity to *Dryas* spp. *Mycologia* 103: 1124–1132. <https://doi.org/10.3852/11-018>
- Ronquist F, Teslenko M, Mark P van der, Ayres DL, Darling A, Höhna S, Larget B & al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542. <https://doi.org/10.1093/sysbio/sys029>
- Schaeffer, JC. 1774. *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur*. 4:21.
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, and Fungal Barcoding Consortium. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for *Fungi*. *Proceedings of the National Academy of Sciences of the United States of America* 109: 6241–6246. <https://doi.org/10.1073/pnas.1117018109>
- Scopoli AG. 1772. *Flora Carniolica*, ed. 2, 2: 457–458. Paul Kraus, Vienna.
- Singer R. 1949. *Mycoflora australis*. *Beihefte zur Nova Hedwigia* 29. 405 p.
- Singer R. 1961. Type studies on Basidiomycetes X. *Persoonia* 2: 1–62.
- Sibthorpe J. 1794. *Flora Oxonensis*. Fletcher & Hanwell, Oxford. <https://doi.org/10.5962/bhl.title.114892>
- Sommerfeldt C. 1826. *Supplementum Florae Lapponicae*. Borg & Gröndahl, Christiniaie.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Tang LP, Hao YJ, Cai Q, Tolgor B, Yang ZL. 2014. Morphological and molecular evidence for a new species of *Rhodotus* from tropical and subtropical Yunnan, China. *Mycological Progress* 13: 45–53. <https://doi.org/10.1007/s11557-013-0890-x>
- Taylor JW. 2011. One fungus = one name: DNA and fungal nomenclature twenty years after PCR. *IMA Fungus* 2: 113–120. <https://doi.org/10.5598/imafungus.2011.02.02.01>
- Thorn RG, Kim JI, Lebeuf R, Voitek A. 2017. The golden chanterelles of Newfoundland and Labrador: a new species, a new record for North America, and a lost species rediscovered. *Botany* 95: 547–560. <https://doi.org/10.1139/cjb-2016-0213>

- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS & al. (eds). 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. <https://doi.org/10.12705/Code.2018>
- Vahl M. 1790. Flora Danica 6(17): pl. 961–1020. København.
- Vizzini A, Ercole E, Voyron S. 2012. *Laccariopsis*, a new genus for *Hydropus mediterraneus* (*Basidiomycota*, *Agaricales*). Mycotaxon 121: 393–403. <https://doi.org/10.5248/121.393>
- Voitk A. 2021. Gratitude for a new attitude to the platitude about latitude and altitude. Omphalina 12: 121–125.
- Voitk A. 2022. Typification of *Agaricus cespitosus*, *Ag. oniscus*, and *Ag. sphagnicola*, and their synonymy with *Lichenomphalia umbellifera*. Mycotaxon 136: 789–818. <https://doi.org/10.5248/136.789>
- Voitk A, Voitk T. 2020. The *Chromosera* of Newfoundland and Labrador. Omphalina 11: 28–35.
- Voitk A, Saar I, Lebeuf R, Kennedy P. 2020. The *Pseudoomphalina kalchbrenneri* complex in North America. Botany 98(2): 91–101. <https://doi.org/10.1139/cjb-2019-0011>
- Voitk A, Saar I, Moncada B, Lickey EB. 2022. Circumscription and typification of sphagnicolous omphalinoid species of *Arrhenia* (*Hygrophoraceae*) in Newfoundland and Labrador: three obligate and one facultative species. Mycological Progress 21(6): 57. <https://doi.org/10.1007/s11557-022-01806-z>
- Vu D, Groenewald M, de Vries M, Gehrman T, Stielow B, Eberhardt U & al. 2019. Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. Studies in Mycology 92: 135–154. <https://doi.org/10.1016/j.simyco.2018.05.001>
- Wahlenberg G. 1826. Flora suecica, vol. 2. Palmblad, Uppsala.
- Wilson AW, Desjardin DE. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (*Basidiomycetes*, euagarics clade). Mycologia 97: 667–679. <https://doi.org/10.1080/15572536.2006.11832797>